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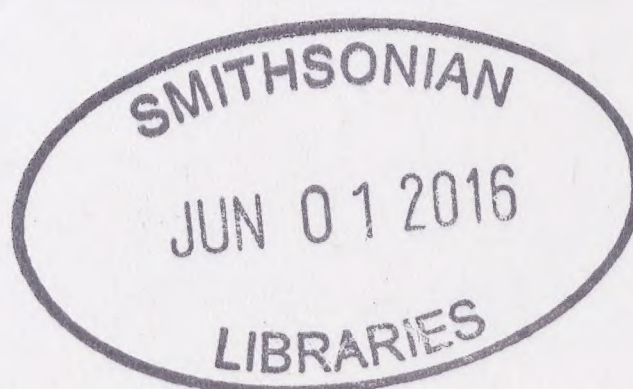
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Outstanding Student Publication Award

The Board of Directors of the Institute of Malacology, publisher of the academic journal *Malacologia*, is pleased to announce the creation of the J Frances Allen Institute of Malacology Outstanding Publication Award. This cash award of \$500 will be presented for an outstanding paper published in *Malacologia* by a student, with the timing dependent on the superior quality of the student paper as judged by a committee of the IM Board. There is no formal application or deadline. A student submitting a manuscript must be sole or senior author of the paper, and should indicate that the paper being submitted stems from Master's or Ph.D. research to confirm his or her eligibility for the award. The Allen Publication Award was established in 2011 to honor J Frances "Jady" Allen, who provided indispensable help and guidance in establishing the journal *Malacologia*, first published in 1962.



ANNOUNCING THE J FRANCES ALLEN INSTITUTE OF  
MALACOLOGY OUTSTANDING STUDENT PUBLICATION AWARD  
FOR 2015

The Board of Directors of the Institute of Malacology, publisher of *Malacologia*, is pleased to announce that Andrew McElwain (currently Visiting Assistant Professor, Department of Biological Sciences, State University of New York at Oswego) has been selected as the 2015 recipient of the J Frances Allen Institute of Malacology Outstanding Publication Award for the paper (with Stephen A. Bullard as co-author) "Histological atlas of freshwater mussels (Bivalvia, Unionidae): *Villosa nebulosa* (Ambleminae: Lampsilini), *Fusconaia cerina* (Ambleminae: Pleurobemini) and *Strophitus connasaugaensis* (Unioninae: Anodontini)." Published in *Malacologia* 57(1): 99–239.

Andrew is the third recipient of this award. His manuscript was selected from among eight outstanding student entries published during the 2014–2015 calendar years. The selection committee was comprised of three members of the Board of Directors of the Institute of Malacology.

Any sole- or senior co-authored publication by an undergraduate or graduate student (or just graduated student) was eligible for consideration. Selection criteria included originality, study design, methods, quality of prose and figures, and potential impact of the publication. The award is made when at least seven full length student papers have been published since the last awardee was selected. The award includes \$500.00 U.S.

Andrew McElwain  
Department of Biological Sciences  
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His dissertation title is "Histological atlas of freshwater mussels (Bivalvia: Unionidae) with comparison of Alabama rainbow (*Villosa nebulosa*), Gulf pigtoe (*Fusconaia cerina*), and Alabama creekmussel (*Strophitus connasaugaensis*), from the Mobile River Basin, Alabama." Dr. Stephen (Ash) Bullard, was his major professor in the Department of Fisheries and Allied Aquacultures (now called "The School of Fisheries, Aquaculture, and Aquatic Sciences" in the College of Agriculture) at Auburn University, in Auburn, Alabama. He graduated from Auburn University with a Ph.D. in Fisheries and Allied Aquacultures in December 2013. In his current position he teaches general zoology, ichthyology, parasitology, histology and conducts research with undergraduate students. He is presently interested in learning more about the relationships between metazoan parasites and their molluscan hosts at the cellular level. Specifically, he is investigating the cellular changes associated with parasites of freshwater mollusks.

Diarmaid Ó Foighil

*Diarmaid Ó Foighil*

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## ULTRASTRUCTURAL AND HISTOLOGICAL STUDY OF OOGENESIS AND OOCYTE DEGENERATION IN THE PENSHELL *ATRINA MAURA* (BIVALVIA: PINNIDAE)

Marian A. Camacho-Mondragón<sup>1</sup>, Bertha P. Ceballos-Vázquez<sup>1</sup>, Esther Uría-Galicia<sup>2</sup>, Edgar O. López-Villegas<sup>2</sup>, Richard Pipe<sup>3</sup> & Marcial Arellano-Martínez<sup>1\*</sup>

### ABSTRACT

The successive stages of oogenesis and the changes involved in the oocyte degeneration process in the penshell *Atrina maura* were examined using light and transmission electron microscopy. The ovarian maturation process is asynchronous, as oocytes at different developmental stages can be found simultaneously. Oocytes develop from oogonia and then undergo three distinct stages of oogenesis: previtellogenesis, vitellogenesis and postvitellogenesis with mature oocytes. *Atrina maura* displays a solitary oogenesis type, in which follicular cells become associated with oocytes from the earliest stages of development and seem to play an integral role in vitellogenesis. The cytoplasm of vitellogenic oocytes contains numerous whorls of rough endoplasmic reticulum and Golgi bodies, suggesting that auto-synthetic vitellogenesis may occur in this species. In addition, the degeneration process of postvitellogenic oocytes triggered by a seasonal increase in water temperature ( $> 25^{\circ}\text{C}$ ) is described.

Key words: vitellogenesis, follicle cell, atresia, resorption, solitary oogenesis type.

### INTRODUCTION

Studies on the reproductive biology of bivalves necessarily start by describing the gonadal organization and gametogenesis (Eckelbarger & Davis, 1996; Erkan, 2009). The study of gametes provides basic knowledge on gametogenesis, including its morphology and stages of development (Raven, 1958; Sastry, 1979). While it is a continuous process, three phases of oogenesis are generally distinguished: previtellogenesis, vitellogenesis and postvitellogenesis (or mature) oocytes. In general, the three phases can be classified by the level of uptake of vitellogenin or yolk protein via microvilli (De Gaulejac et al., 1995). Furthermore, with the information obtained from ultrastructure studies on oogenesis, it is even possible to infer the nutritional strategy during the early stages of larval development, as this is directly related to the amount of yolk present and the size of postvitellogenic oocytes (Beninger & Le Pennec, 1997).

Ultrastructural studies of oogenesis have been conducted in a number of bivalve spe-

cies, particularly those of economic importance (Pipe, 1987; Dorange & Le Pennec, 1989; Chung et al., 2007; Lee & Chung, 2008; Erkan, 2009; Glavinic et al., 2012). These studies have focused mainly on changes occurring during vitellogenesis in each species, particularly the role of follicular cells in this process. Furthermore, these investigations describe the oocyte degeneration process (atresia) that usually takes place in one of the stages of the “normal” gonadal cycle in these organisms. Within the family Pinnidae, the entire oogenesis process has been described at the ultrastructural level only for *Pinna nobilis* (Linnaeus, 1758) (De Gaulejac et al., 1995). In *Atrina maura* (G. B. Sowerby I, 1835) (Enriquez Diaz et al., 2003) and *A. pectinata* (Linnaeus, 1767) (Fang & Qi, 1988), only some stages of gametogenic development have been described at the ultrastructural level for specimens maintained under controlled laboratory conditions. Clearly, there is still scarce information about several aspects, that is, the morphology of cytoplasmic organelles throughout the oogenesis process under natural conditions, the various compounds that

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accumulate during the vitellogenesis process, and the changes that occur in atretic oocytes.

*Atrina maura* is a commercially important species that, for several decades, has constituted an abundant natural resource across the temperate and tropical coasts of the Mexican Pacific (Vélez-Barajas & Fajardo-León, 1996; Ahumada-Sempoal et al., 2002). However, fishermen in Baja California Sur, Mexico, have recently reported a marked decline in the abundance of this species in several fishing areas (fishermen from Mangle Cenizo Cooperative Society, pers. comm.). For this reason, several research institutions have conducted unsuccessful trials to produce seed of *A. maura* under laboratory conditions to meet the market demand and launch repopulation activities (Silvia Ramírez, Noroeste Sustentable, A. C., pers. comm.). In this sense, basic knowledge about the reproductive biology of this species is key for successfully rearing it under controlled conditions.

The objective of this study is to provide a detailed ultrastructural description of the stages of female gamete formation in *A. maura* and, particularly, of the degeneration process (atresia) of postvitellogenic oocytes. Follicular cells involved in both processes are also examined.

## MATERIALS AND METHODS

Adult female specimens (> 12 cm shell length) of *Atrina maura* were collected at the Ensenada de La Paz coastal lagoon (24°06'N–24°11'N and 110°19'W–110°26'W), Baja California Sur, Mexico. Since previous studies under controlled temperature conditions (Rodríguez-Jaramillo et al., 2001) and in wild populations (Camacho-Mondragon et al., 2012) found a relationship between temperature above 25°C and the resorption of oocytes, sampling was conducted during January (21°C) and September (30°C) in order to describe the ultrastructure of both viable and degenerating oocytes (atresia).

Specimen gonads were dissected and processed for transmission electron (TEM) and light (LM) microscopy examination. For TEM, approximately 5-mm thick sections were obtained and fixed in 2.5% glutaraldehyde (Electron Microscopy Sciences) in seawater with a pH of 8 for 6 h, then rinsed with a Sorensen's phosphate buffer solution and post-fixed with 1% osmium tetroxide for one h. Dehydration

was performed using a sequence of ethanol solutions of increasing concentration (70 to absolute). Tissues were infiltrated with a propylene oxide solution and epoxy resin for three h and then embedded in EPON 812 resin. Ultrathin, 70 nm-thick sections were obtained with an ultramicrotome and then stained for contrast with uranyl acetate and lead citrate. Finally, sections were examined under a Jeol-100SX (60000 V) transmission electron microscope and micrographs of different portions of the gonad were obtained. In parallel, LM samples were fixed in 10% formalin in seawater and processed using conventional histological techniques (Humason, 1979), including dehydration with an increasing-concentration sequence of ethanol solutions followed by clearing with Hemo-De® and embedding in Paraplast-Xtra®. Five µm-thick sections were obtained, which were then stained with Hematoxylin-Eosin.

The information obtained from LM and TEM examinations was used to describe the stages of oogenesis at different levels. LM observations provided an overview of the ovarian structure which allowed the observation of the arrangement of gametes within the acini at different developmental stages. These observations, in turn, supplement the detailed descriptions obtained through TEM, which occasionally may overlook important features by focusing on highly specific areas due to the technique's inherent characteristics. Finally, measurements of total gamete and nucleolar diameters were obtained for all the development stages.

## RESULTS

### General Morphology of Gonadal Tissue and Oocytes

The ovary of *Atrina maura* consists of several clusters of highly branched globular acini surrounded by a thin acinar wall. During oogenesis, each acinus contains oocytes in different stages of development. Developing oocytes are in close contact with the follicular cells, whereas postvitellogenic oocytes are free in the acinar lumen (Fig. 1).

LM and TEM observations allowed the identification of four oocyte development stages: oogonia, previtellogenesis, vitellogenesis and postvitellogenesis. All stages were observed in January (21°C) and September (30°C). However, a high frequency of atresia in post-



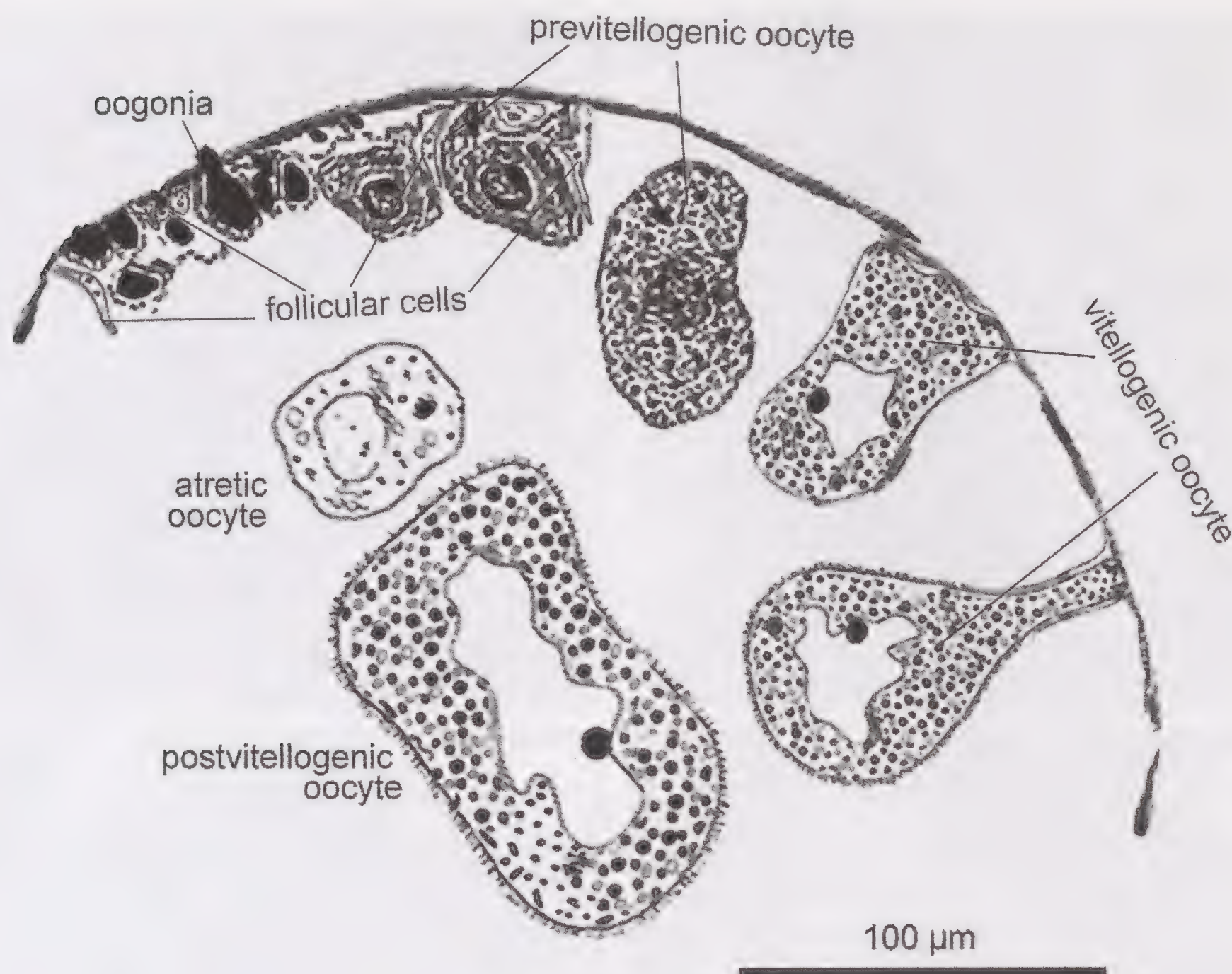


FIG. 1. Schematic representation of oogenesis in *Atrina maura*, based on light and transmission electron microscopy observations. The stages of oogenesis are oogonia and previtellogenic, vitellogenic and postvitellogenic oocytes. Oocyte atresia is also shown.

vitellogenic oocytes was observed during September.

In *A. maura*, the association of follicular cells with developing oocytes was observed only during the early stages of oogenesis, when follicular cells were located very close to oogonia (Fig. 4). Postvitellogenic oocytes were characterized by a significantly larger diameter (twice that of vitellogenic oocytes) and a spherical shape. As oocyte diameter increases, oocytes aggregate at the lumen center. In mature ovaries, the lumen is filled with postvitellogenic oocytes, and no follicular cells are associated with oocytes undergoing the intermediate or advanced stages of oogenesis.

#### Oogonia

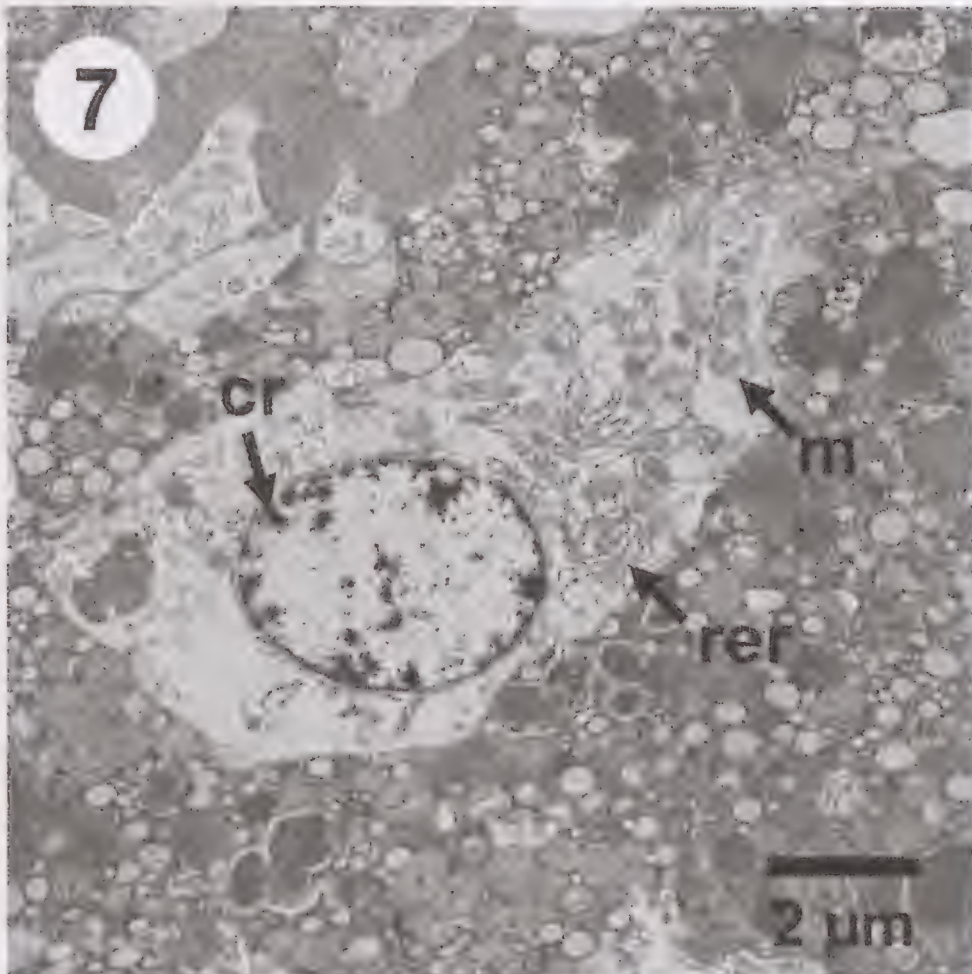
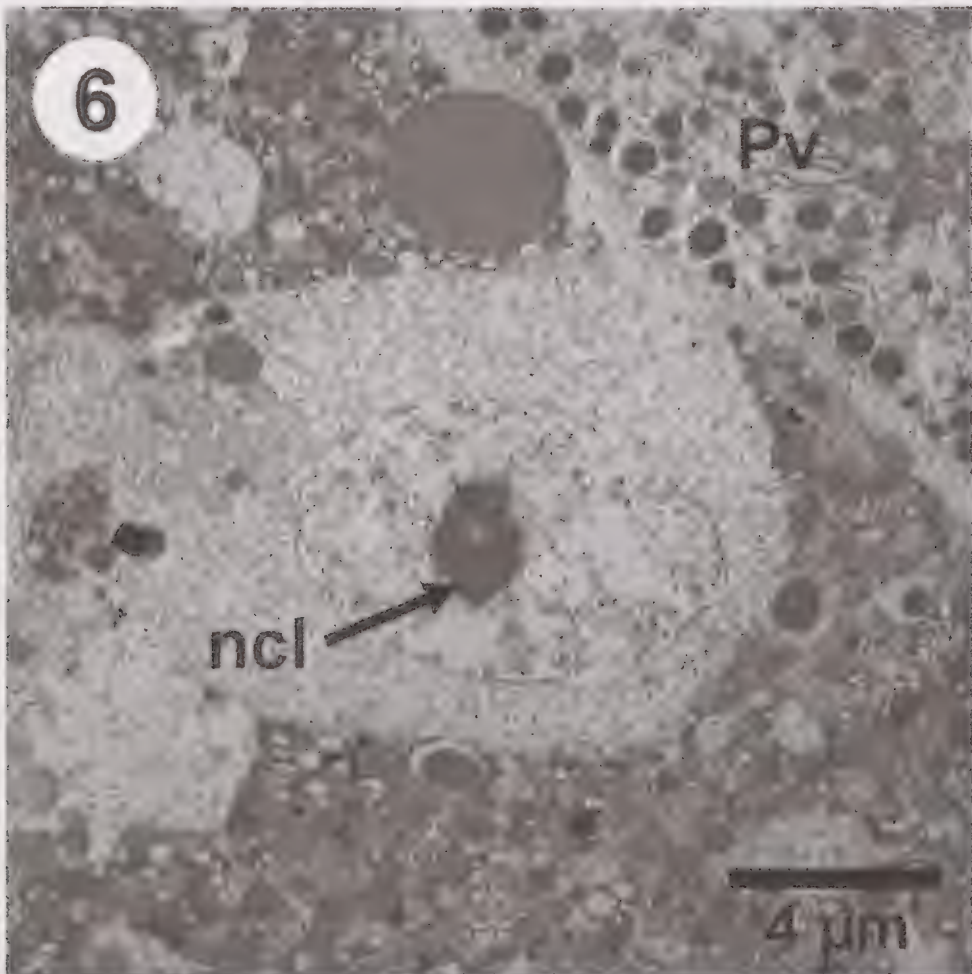
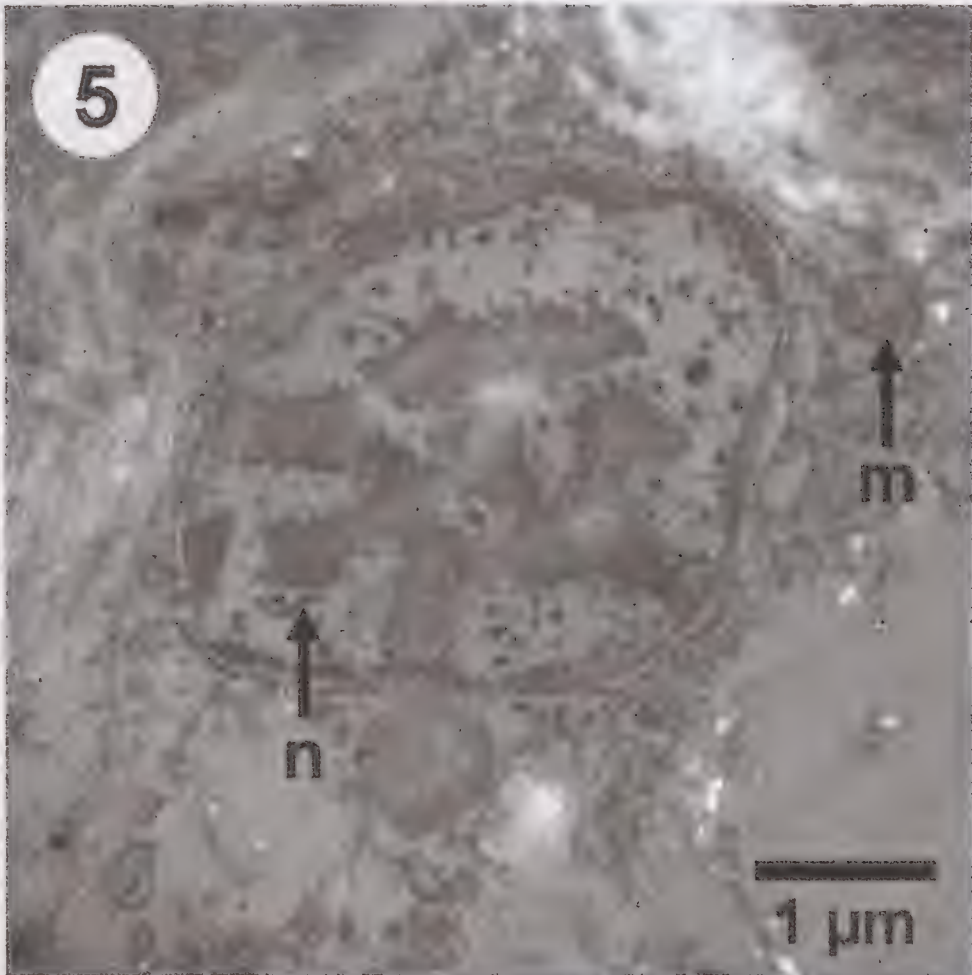
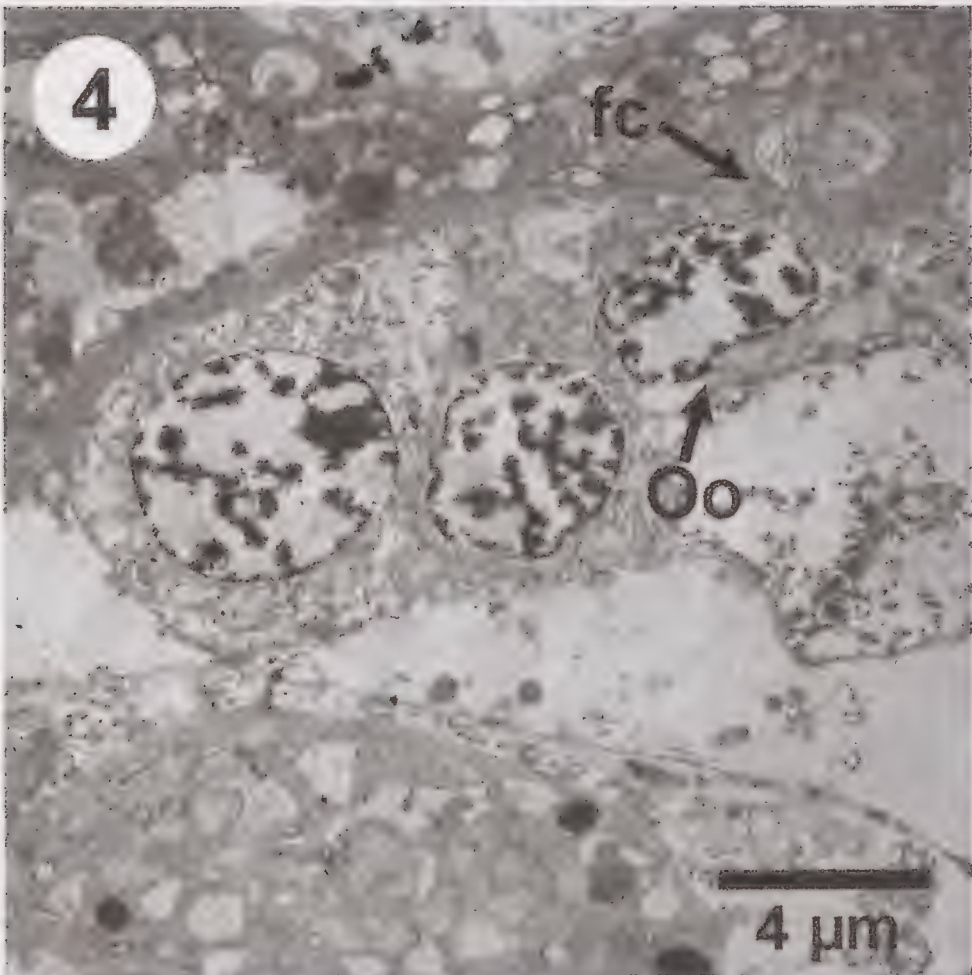
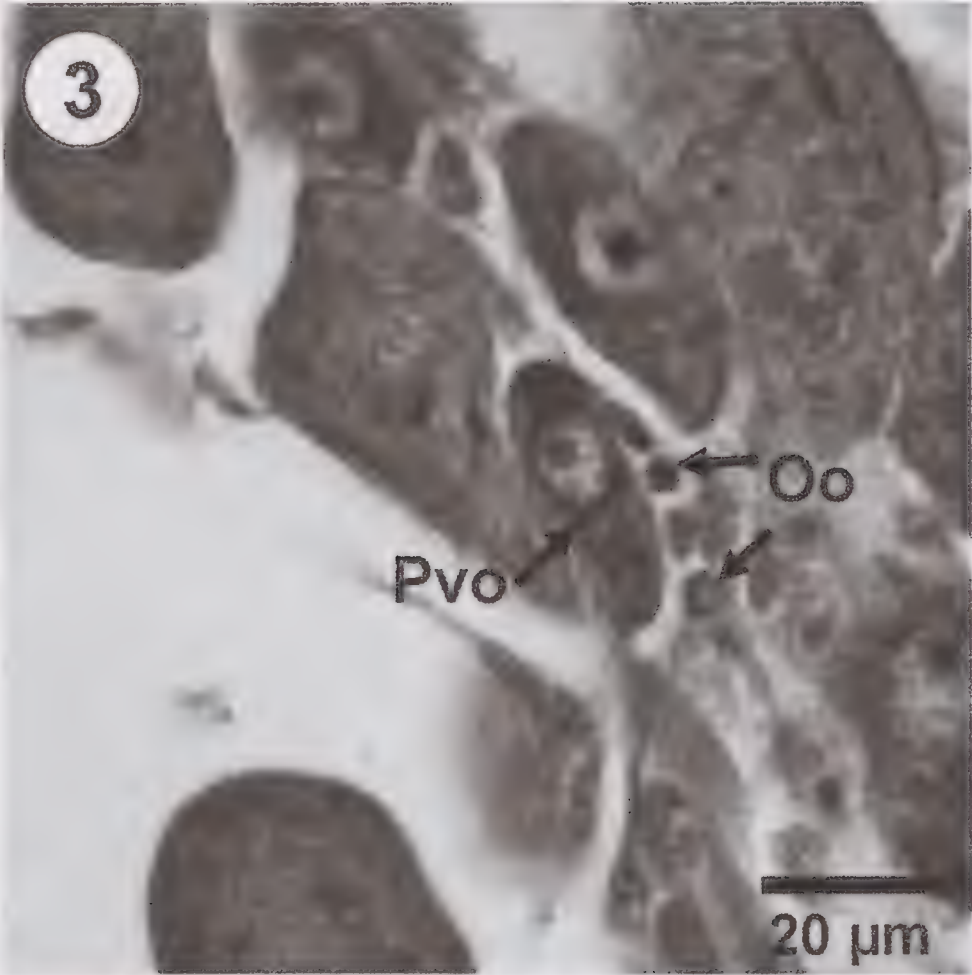
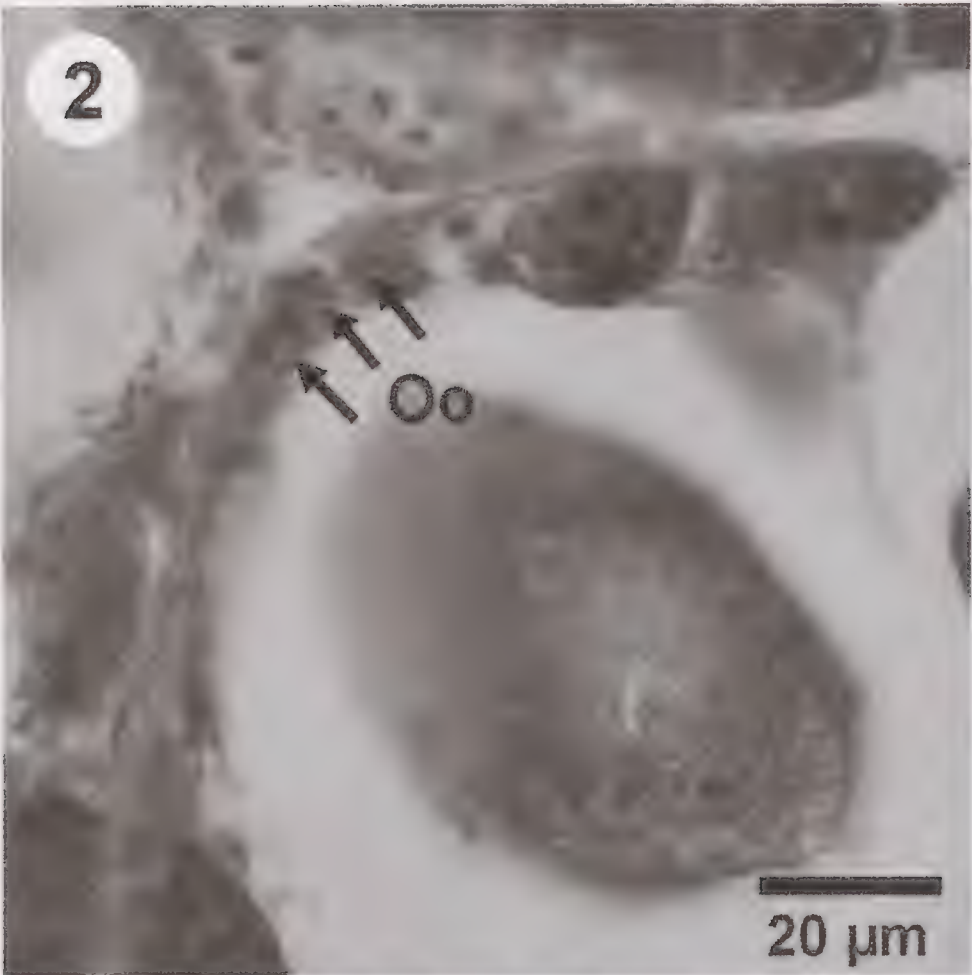
In *A. maura*, oogonia occur as one- or two-cell layers that cover the inner acinus wall (Figs. 2–5), either in direct contact or separated from the edge by pseudopodia-like projections of follicular cells (Fig. 4). Oogonia are round or elongated and measure between 6 and 10  $\mu\text{m}$ .

Typically, oogonia show a high nucleus-cytoplasm ratio and the round and large nucleus is more basophilic than the cytoplasm (Figs. 2, 3) containing numerous spherical mitochondria (Fig. 5). TEM revealed that oogonia frequently have a large nucleus with reticular, marginally located chromatin and a single nucleolus (Figs. 6, 7). Also present are numerous ribosomes, Golgi apparatus, some cisternae of the rough endoplasmic reticulum, lipid droplets and dense aggregates in the cytoplasm (Fig. 7).

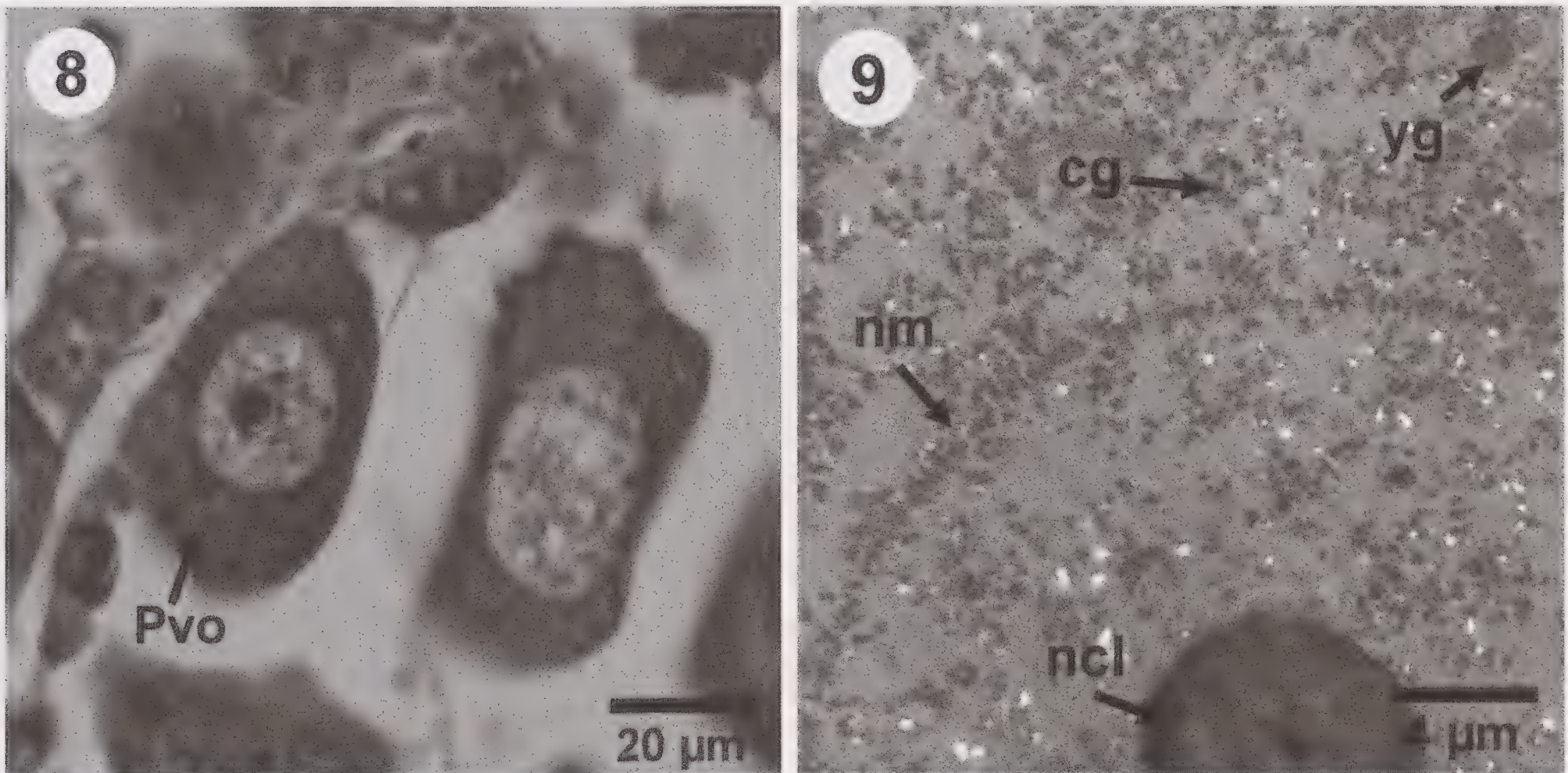
#### Previtellogenic Oocytes

Previtellogenic oocytes can reach up to 30  $\mu\text{m}$  in diameter, with irregular edges and a nucleolus measuring 5  $\mu\text{m}$  in diameter (Figs. 8, 9). LM showed that previtellogenic oocytes have a basophilic nucleus and a slightly eosinophilic cytoplasm (Fig. 8). TEM images showed a well-defined nuclear membrane and a cytoplasm with a larger volume but containing few organelles. Previtellogenic oocytes are still close to one another, but no desmosomes









FIGS. 8–9. Light (8) and transmission electron microscopy (9) images of previtellogenic oocytes in *Atrina maura*. FIG. 8: Previtellogenic oocyte (Pvo) in the acinus wall; FIG. 9: Previtellogenic oocyte with a well-defined nuclear membrane (nm) and nucleolus (ncl); numerous cortical (cg) and some yolk (yg) granules can be observed in the cytoplasm.

were observed. Numerous cortical granules aggregated in the cytoplasm were observed, along with the appearance of the first yolk granules. Neither microvilli nor a vitelline layer were present at this stage (Fig. 9).

#### Vitellogenic Oocytes

Oocytes entering the vitellogenesis stage continue growing while migrating into the acinar lumen by accumulating yolk granules in the cytoplasm and reach diameters ~ 40 μm. The junction with the acinus wall, known as the stem, displayed numerous clustered mitochondria and was visible only through LM (Fig. 10). TEM images reveal lightly-electron dense yolk granules of a similar electron density as the vitelline layer. Lipid granules had a much more electrondense consistency (Fig. 11). Common structures in vitellogenic oocytes are Balbiani's vitelline bodies or yolk nuclei (De Gaulejac et

al., 1995), which develop significantly as vitellogenesis progresses (Figs. 12, 13). The nucleus of vitellogenic oocytes is round and often displays several dense accumulations near the nuclear membrane; only one nucleolus is present (Fig. 14). Microvilli appear for the first time in the final vitellogenesis stage; cytoplasmic organelles proliferate and numerous whorls of rough endoplasmic reticulum (rer) are apparent throughout the cytoplasm (Fig. 15).

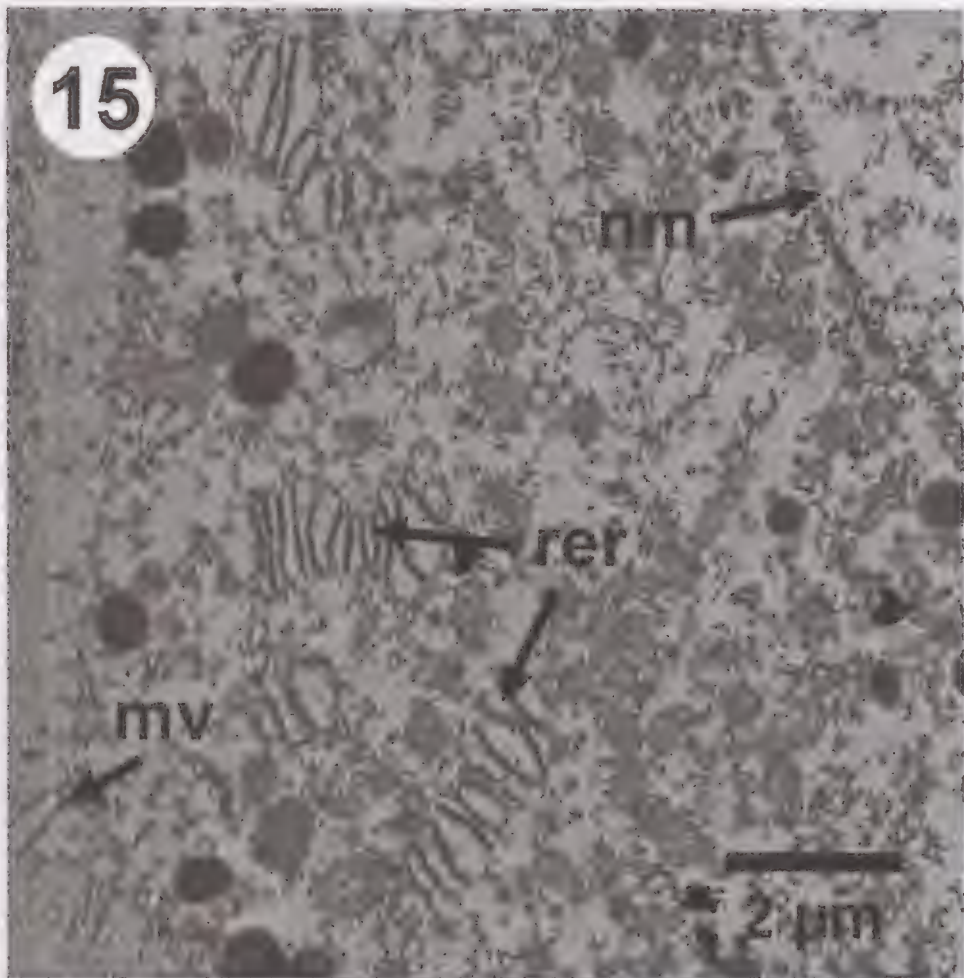
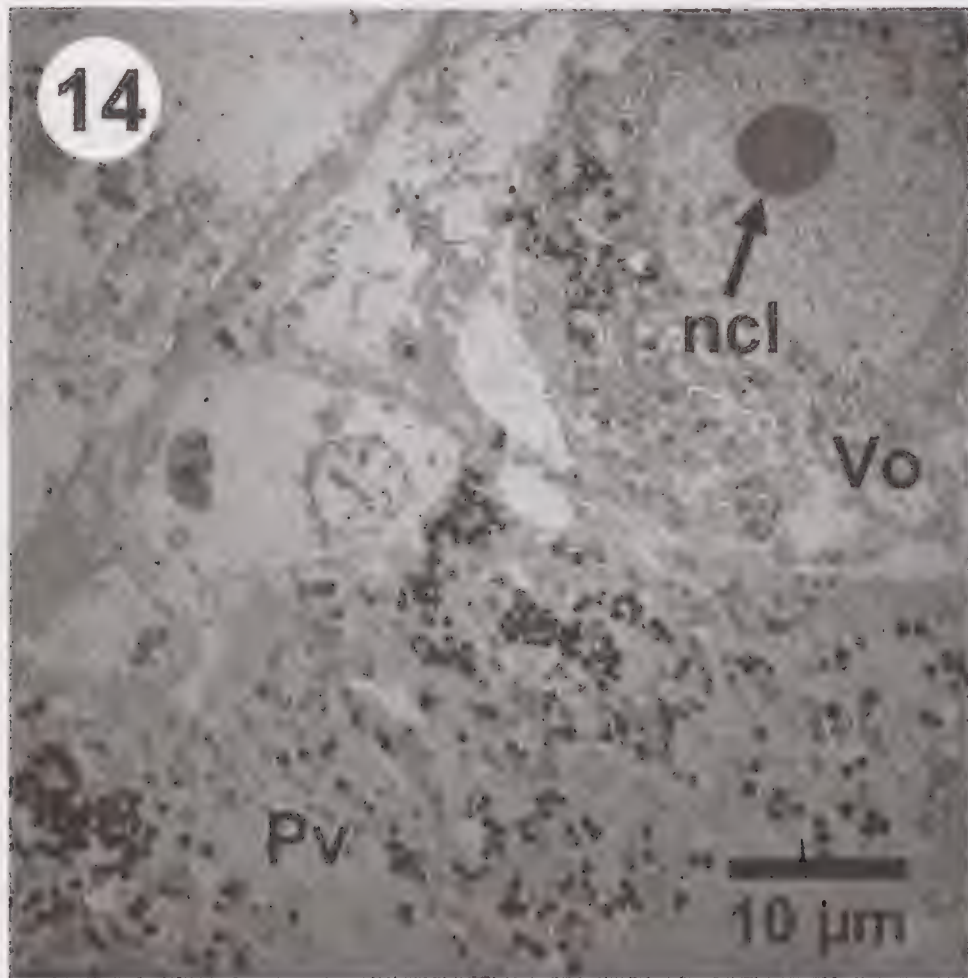
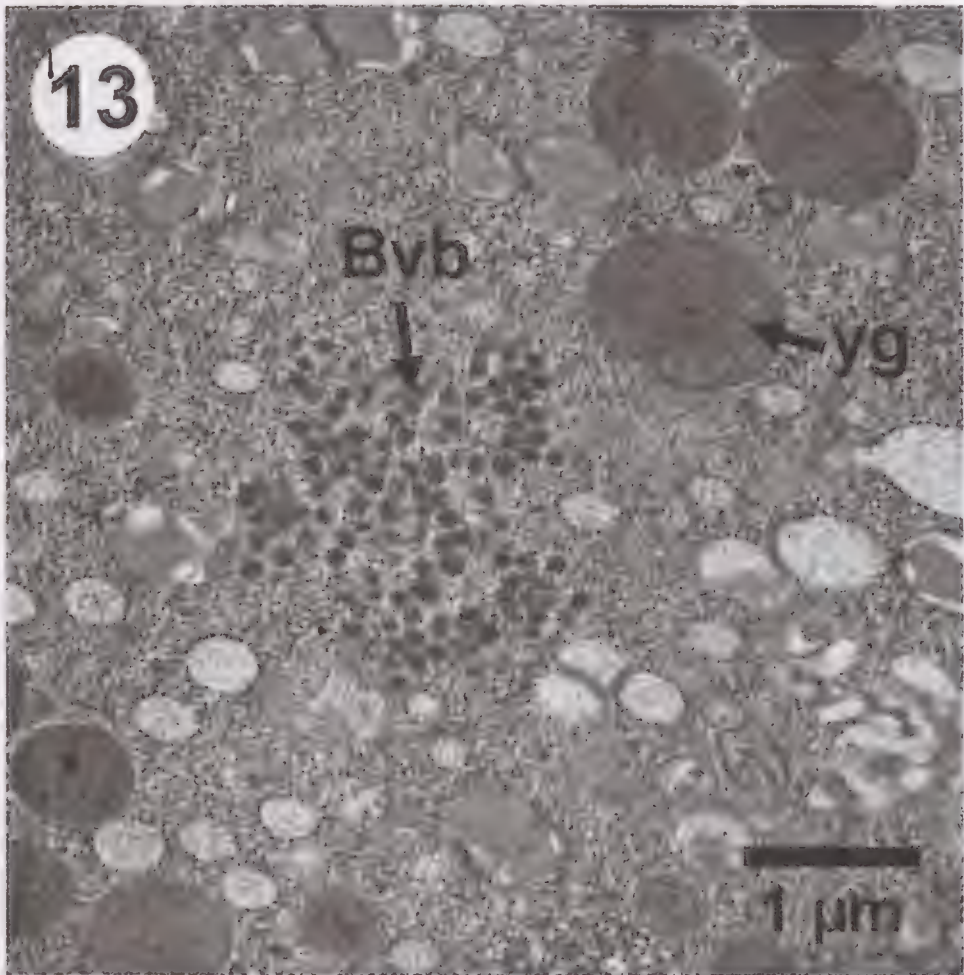
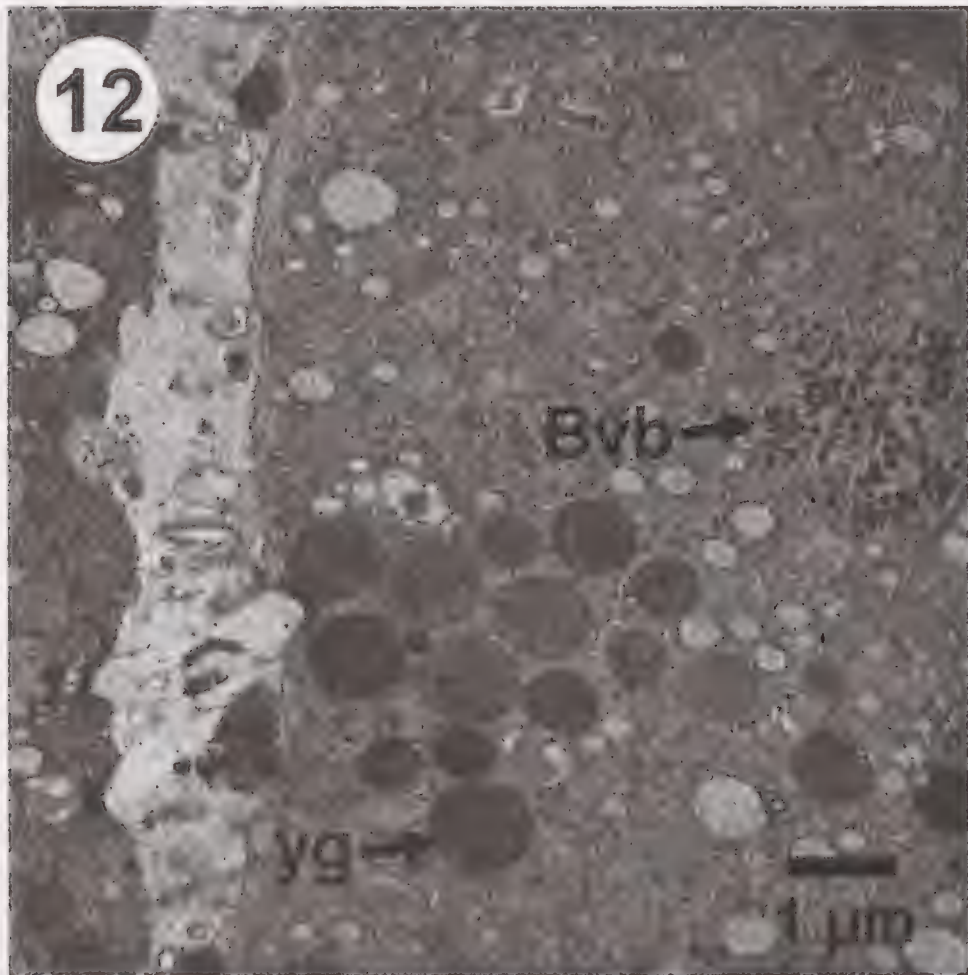
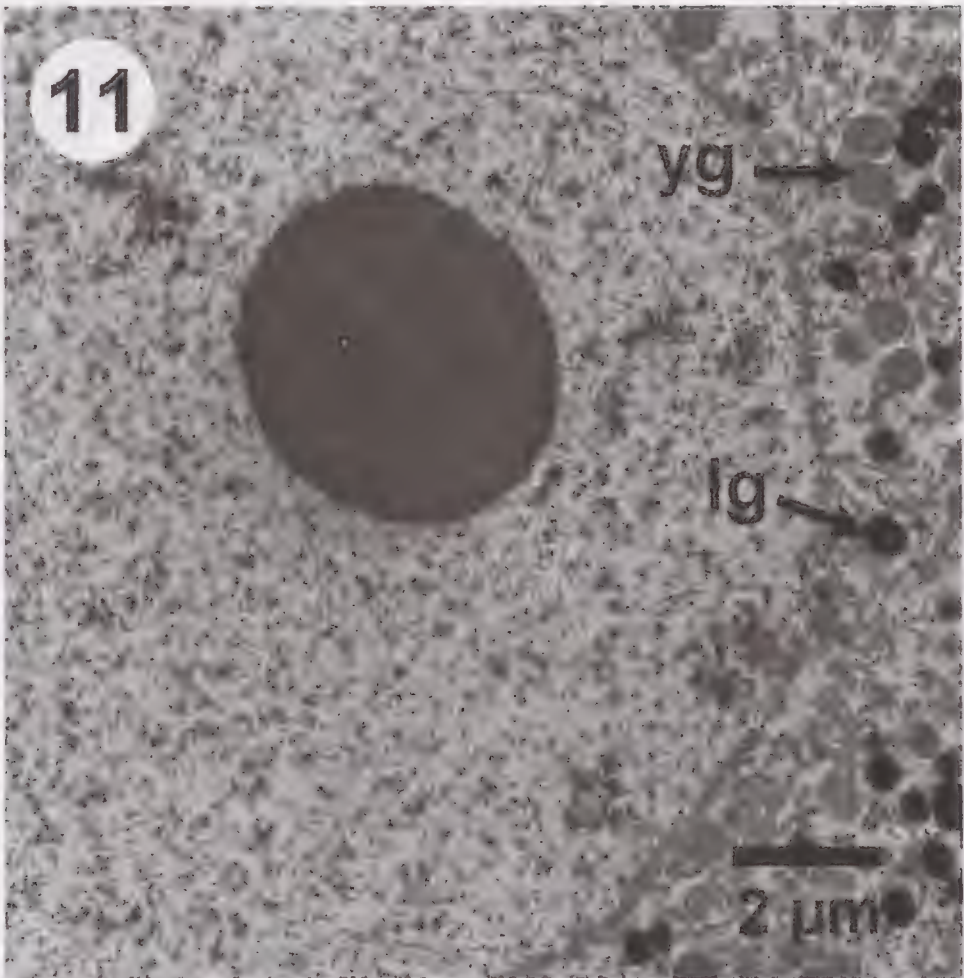
#### Postvitellogenic Oocytes

Postvitellogenic oocytes reach up to 80 μm in diameter, have a polyhedral appearance at the acinar lumen and are deformed by compression in the mature gonad (Fig. 16). TEM images showed that postvitellogenic oocytes contain numerous yolk and lipid granules (Fig. 17). No joints between oocytes and follicular cells were observed at this stage. The nucleus is homoge-

←

FIGS. 2–7. Light (2 and 3) and transmission electron microscopy (4–7) images of the early stages of oogenesis in *Atrina maura*. FIG. 2: Oogonia (Oo) located in the acinus wall; FIG. 3: Oogonia next to a previtellogenic oocyte (Pvo) with a distinct nucleus; FIG. 4: Oogonia in contact with a follicular cell (fc); FIG. 5: Close-up of an oogonia showing the nucleus (n) and mitochondria (m); FIG. 6: Oogonia showing the nucleolus (ncl) next to a postvitellogenic oocyte (Pv); FIG. 7: Oogonia with chromatin (cr) on the periphery of the nucleus and a large number of organelles in the cytoplasm, including mitochondria (m) and rough endoplasmic reticulum (rer).







neous, and the nucleolus, generally located in a marginal position but sometimes to the center of the nucleoplasm, appears dense (Fig. 18). The rough endoplasmic reticulum, the tubular end of which appears expanded, has numerous layers stacked close to each other and parallel to the nuclear envelope; this constitutes the annulate lamellae. Mitochondria can be observed throughout the ooplasm, and cortical granules are very numerous at the periphery of these oocytes. Dense aggregates are larger than those seen in vitellogenic oocytes and the Golgi apparatus is evident. At this stage, microvilli are quite visible and completely surround the oocytes (Figs. 19–21).

### Oocyte Degeneration

In atretic postvitellogenic oocytes, the endoplasmic reticulum is expanded, leading to ooplasm vacuolation (Fig. 22); mitochondria degenerate and myelin-like organelles appear (Fig. 23). No Golgi apparatus can be observed in atretic oocytes, the nucleus deteriorates, the nuclear intermembrane space increases and the nuclear envelope breaks down. At the same time, the nucleolus also deteriorates and electron dense accumulations appear in the nucleoplasm. The cytoplasmic membrane disintegrates, but yolk granules and lipid inclusions accumulate, forming a dense globular mass in the acinar lumen (Fig. 24). An increase in the perivitelline space causes microvilli to detach from the oocyte surface. The cytoplasmic membrane and the vitelline layer collapse, and the lytic material is released into the acinar lumen (Fig. 25).

## DISCUSSION

The overall characteristics of the gonad and the oogenesis process in *A. maura* resemble those described for such other bivalves as *Mytilus edulis* Linnaeus, 1758 (Pipe, 1987), *Pecten maximus* (Linnaeus, 1758) (Dorance

& Le Pennec, 1989), *Crassostrea virginica* (Gmelin, 1791) (Eckelbarger & Davis, 1996) and *Cyclina sinensis* (Gmelin, 1791) (Chung et al., 2007), as well as those of their closest relatives *A. pectinata* (Fang & Qi, 1988) and *P. nobilis* (De Gaulejac et al., 1995).

Oogenesis in bivalves is classified as either follicular or solitary (Pipe, 1987; Glavinic et al., 2012.). The least common modality is follicular oogenesis, in which follicular cells completely surround oocytes throughout the development process, and has been reported in only a few species (Ituarte, 2009). In solitary oogenesis, developing oocytes are not completely surrounded by follicular cells, and these only occur during certain development stages. This type of oogenesis has been reported in the family Pinnidae (*A. pectinata*, Fang & Qi, 1988, and *P. nobilis*, De Gaulejac et al., 1995).

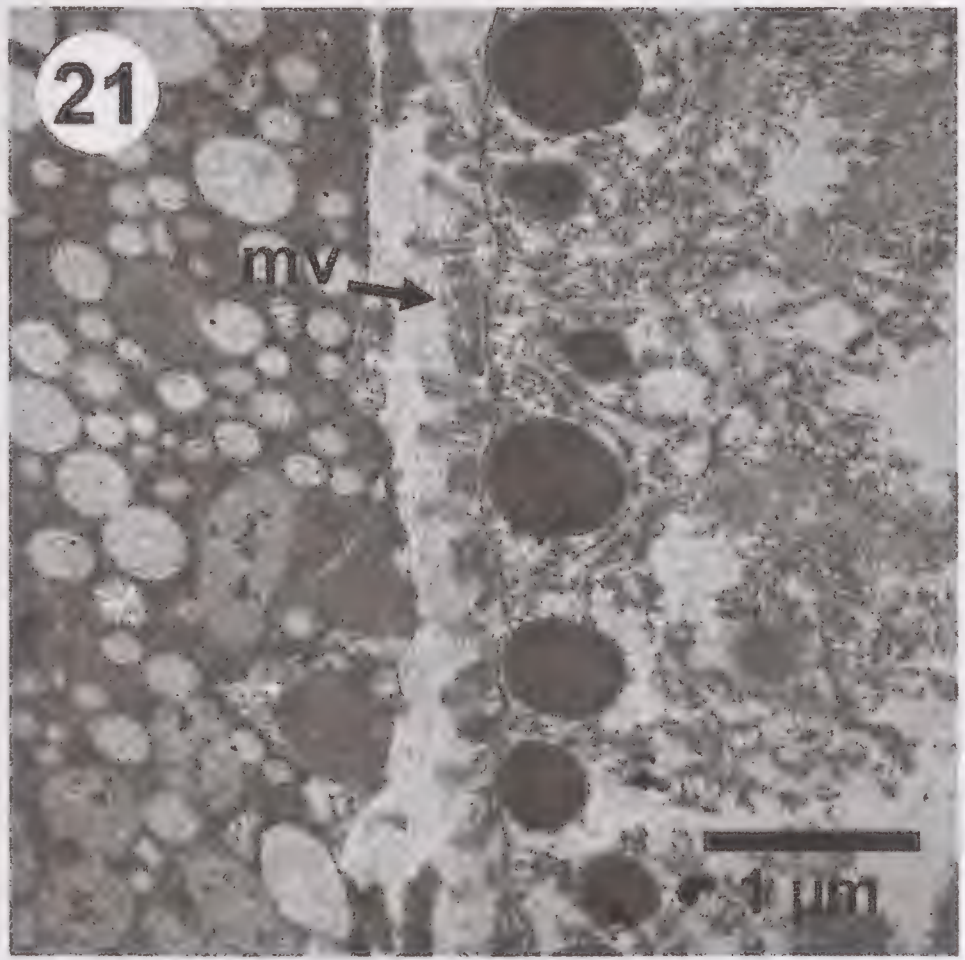
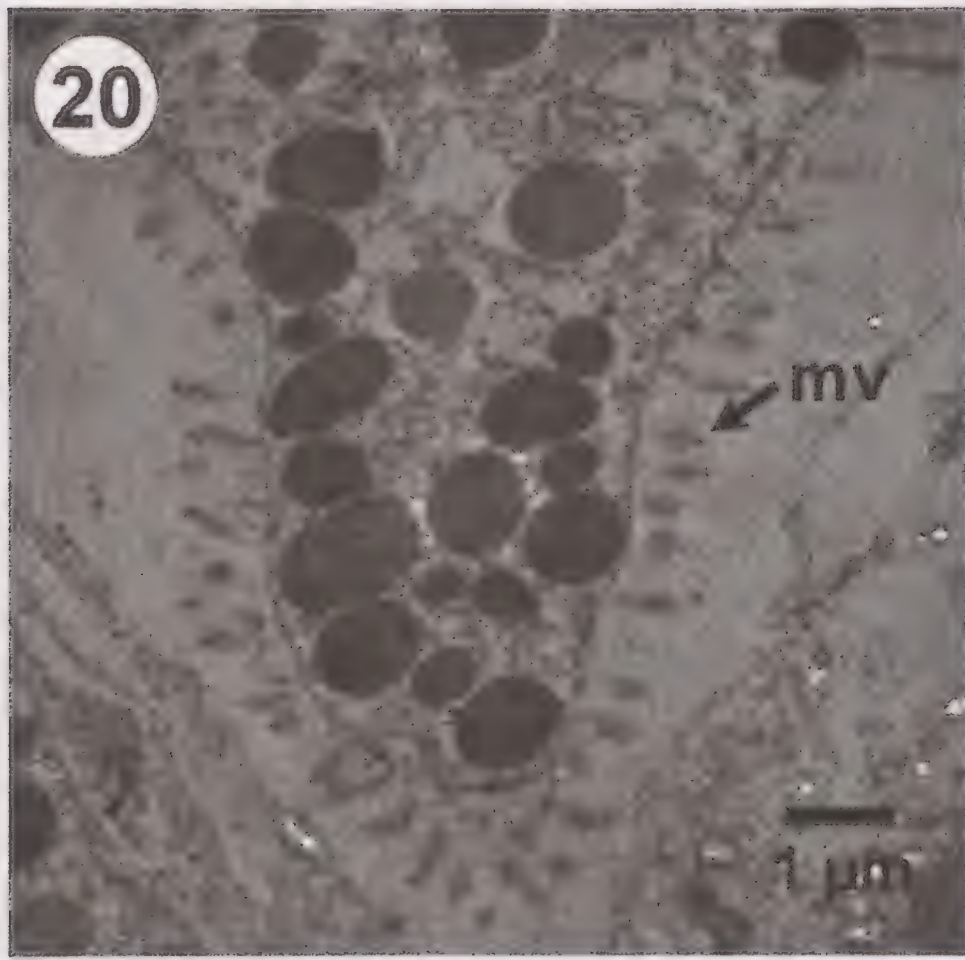
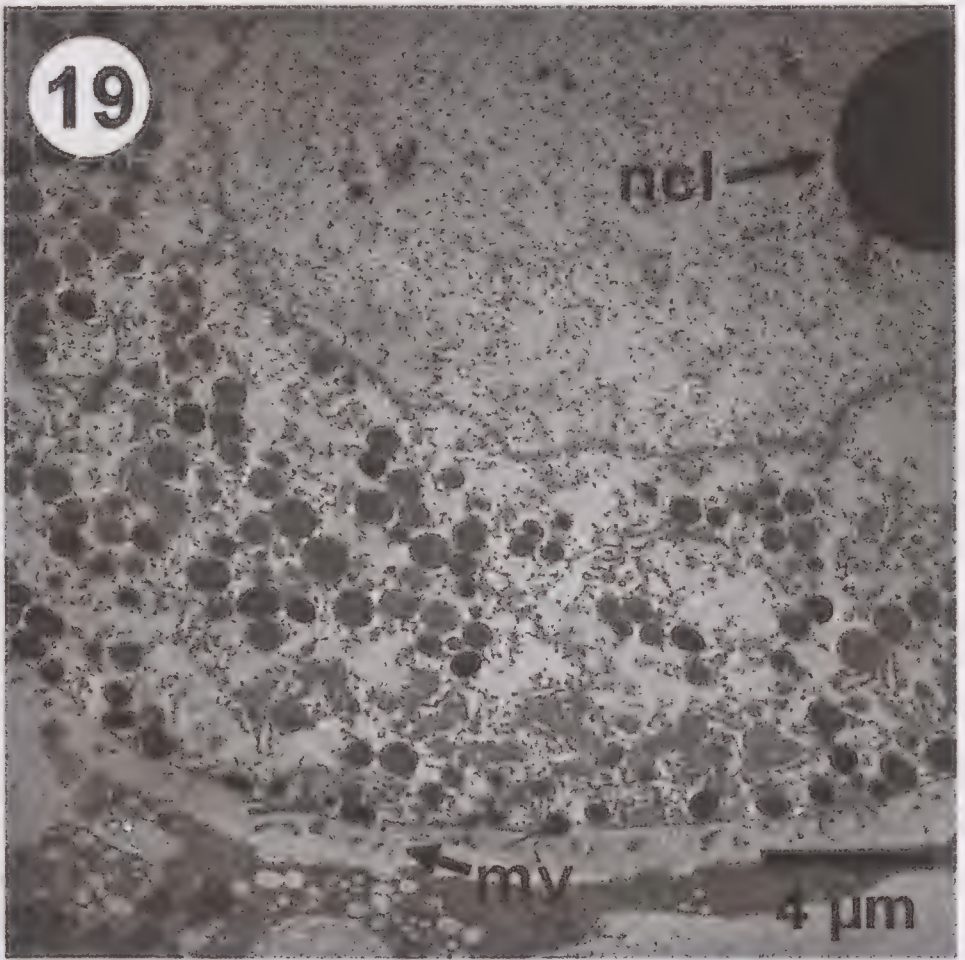
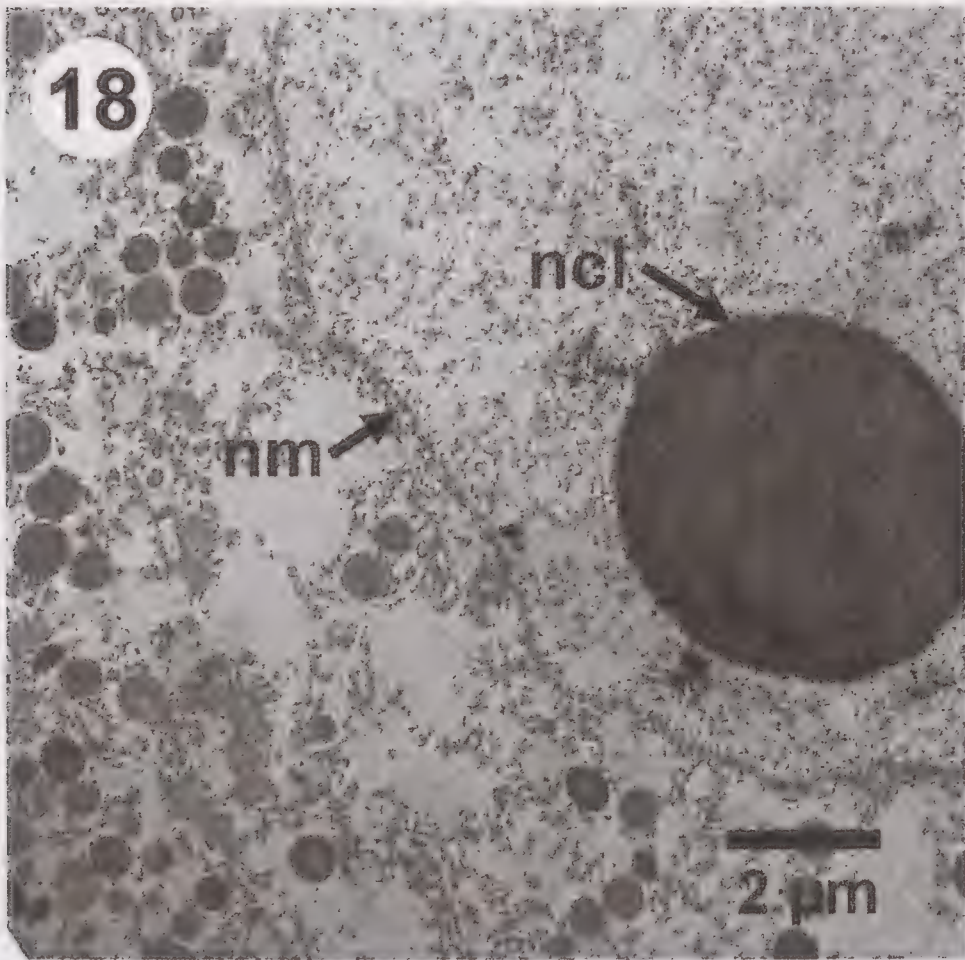
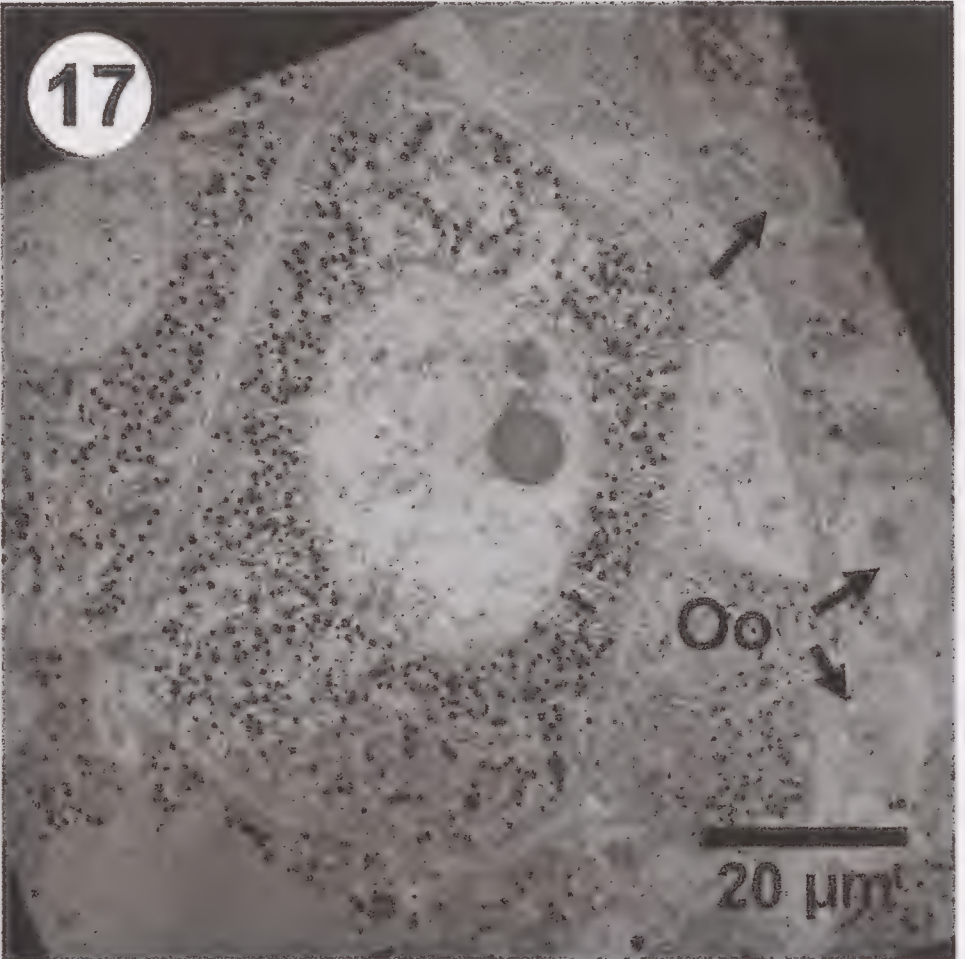
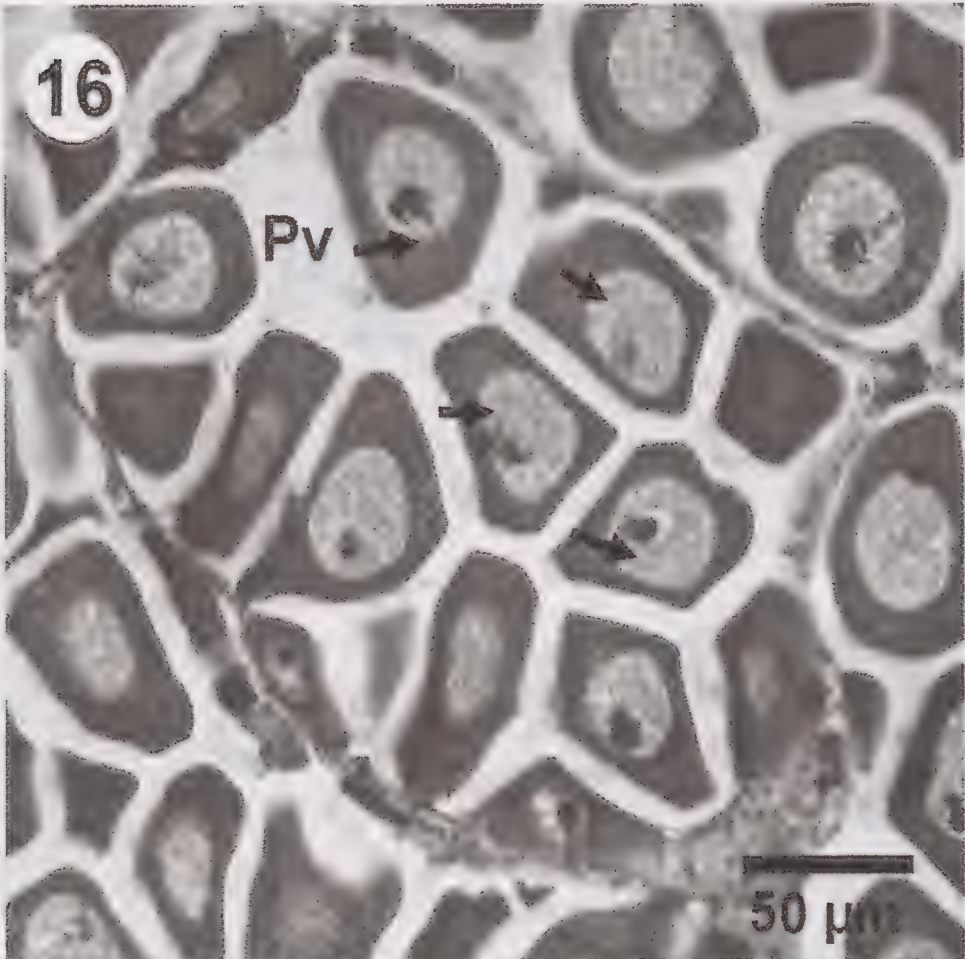
Observations in the present study revealed that *A. maura* displays a solitary-type oogenesis that starts with oogonia followed by previtellogenic, vitellogenic and, finally, postvitellogenic oocytes.

The previtellogenic stage of oogenesis in *A. maura* is characterized by the presence of a well-defined nucleus, cortical granules, numerous mitochondria and ribosomes, and endoplasmic reticulum. In *P. nobilis*, this has been interpreted as the startup of an intense synthetic activity (De Gaulejac et al., 1995). The nuclear envelope is well formed and displays numerous pores that allow the transfer of nutrients to the growing oocytes. During the vitellogenic stage, cytoplasmic growth is mainly due to the accumulation of yolk. For Hill & Bowen (1976), most cytoplasmic organelles are involved and, although the incorporation of exogenous macromolecular substances has been described in many species (Bottke et al., 1982), it appears that the endogenous formation of yolk prevails during the vitellogenic stage in molluscs (de Jong-Brink et al., 1983). Several cytoplasmic constituents have been proposed to be involved in the formation of yolk granules. For *M. edulis* (Pipe, 1987)

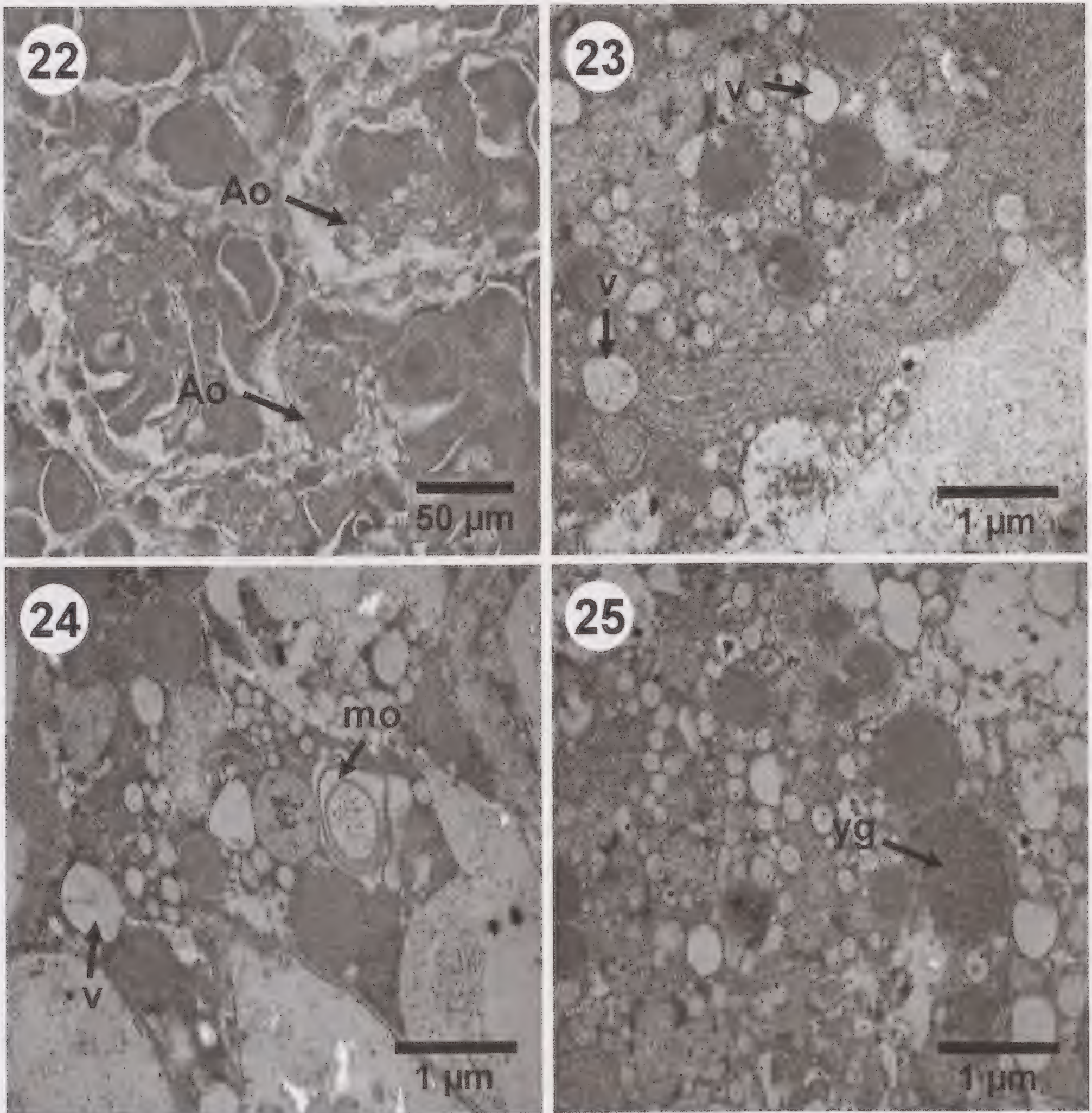
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FIGS. 10–15. Light (10) and transmission electron microscopy (11–15) images of vitellogenic oocytes in *Atrina maura*. FIG. 10: Vitellogenic oocyte being detached from the acinus wall; numerous mitochondria (m) can be observed clustered in the stem; FIG. 11: Detail of cytoplasm containing yolk (grey) (yg) and lipid (black) (lg) granules; FIGS. 12, 13: Balbiani's vitelline body (Bvb) including numerous yolk granules (yg); FIG. 14: Vitellogenic oocyte (Vo) showing the nucleolus (ncl) next to a postvitellogenic oocyte (Pv); FIG. 15: Oocyte in the final vitellogenesis stage; microvilli (mv) can be seen at the periphery, as well as numerous whorls of rough endoplasmic reticulum (rer). nm: nuclear membrane.









FIGS. 22–25. Light (22) and transmission electron microscopy (23–25) images of atretic oocytes in *Atrina maura*. FIG. 22: Atretic oocytes (Ao) with collapsed cytoplasmic membranes emptying their contents into the acini lumen; FIG. 23: Large number of vacuoles (v) in the cytoplasm; FIG. 24: Ooplasm with a myelin-like organelle (mo); FIG. 25: Dense masses formed by yolk granules (yg) in the ooplasm.

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FIGS. 16–21. Light (16) and transmission electron microscopy (17–21) images of postvitellogenic oocytes in *Atrina maura*. FIG. 16: Polyhedral postvitellogenic oocytes (Pv) in the acinar lumen; FIG. 17: Postvitellogenic oocyte showing numerous granules in the cytoplasm; three oogonia (Oo) can be seen at the acinus periphery; FIG. 18: Detail of the nucleus showing the marginal location of the nucleolus (ncl) and its dense appearance. (nm) nuclear membrane; FIG. 19: Postvitellogenic oocyte completely surrounded by microvilli (mv); FIG. 20: Close-up of microvilli (mv) in a deformation of the plasmatic membrane of a postvitellogenic oocyte; FIG. 21: Detail of the numerous microvilli (mv) present in postvitellogenic oocytes.



and *Crassostrea gigas* (Suzuki et al., 1992), an autotrophic formation of yolk protein has been suggested to occur, due to the presence of numerous whorls of endoplasmic reticulum and Golgi bodies in the cytoplasm of oocytes undergoing vitellogenesis. In this sense, our observations suggest that autotrophic vitellogenesis occurs in *A. maura*. In this species, as in *P. nobilis* (De Gaulejac et al., 1995) and *A. pectinata* (Fang & Qi, 1988), the lipid-protein yolk granules are formed by the fusion of lipid globules, expanded cisterns of endoplasmic reticulum and vesicles derived from Golgi bodies. It has been reported that endoplasmic reticulum whorls configurations are characteristic structures common in developing oocytes (Pipe, 1987) and that substances used for the formation of yolk granules likely migrate gradually through the different lamellar rings of the endoplasmic reticulum to finally concentrate in the central area (Reverberi, 1966). Images of *A. maura* show that annular lamellae do occur in vitellogenic oocytes, thus supporting the above reports.

Evidence of the transformation of mitochondria into yolk granules has also been reported for several molluscan species, such as *Planorbis corneus* (Linnaeus, 1758) (Albanese & Bolognari, 1964), *A. pectinata* (Fang & Qi, 1988) and *Patella coerulea* (Linnaeus, 1758) (Benmeradi, 1992). However, in *A. maura* we did not observe such involvement of mitochondria in the formation of yolk. In this species, mitochondria are first seen in oogonia and afterwards multiply during the previtellogenic stage. These organelles were observed forming clusters along the stem of vitellogenic oocytes; this suggests that they supplement microtubules in their role as supporting structures, and possibly delimits the channels through which materials are transferred between different parts of the oocyte (De Gaulejac et al., 1995). In subsequent oogenesis stages in *A. maura*, mitochondria are still present in the cytoplasm, but are not as abundant as in the early stages, suggesting that mitochondrial activity has decreased.

At the beginning of the vitellogenic stage in *A. maura* large lipid droplets appear, but there is no clear morphological evidence about the processes involved in the formation of lipid granules. However, in *A. maura* as well as in other species, lipid droplets may arise from Balbiani bodies through the transformation of mitochondria and other organelles (Dohmen, 1983; Chung et al., 2005). Alternatively, lipids may be produced outside the oocyte – by fol-

licular cells, for example – and be subsequently incorporated by phagocytosis (Dohmen, 1983), or glycogen may be converted into lipids as seen in *M. edulis* (Pipe, 1987).

In *A. maura*, cortical granules are only found in previtellogenic oocytes. Firstly, these are randomly distributed but, as vitellogenesis progresses, they migrate to the oocyte periphery; this has been suggested as a strategy to prevent polyspermy by releasing their contents during fertilization (Pipe, 1987). It is known that granules are composed of glycoprotein, but their origin is poorly understood. In *M. edulis*, cortical granules often appear in clusters during oocyte development, apparently with membrane connections, and may also increase in number by division (Pipe, 1987).

It has been reported that massive atresia of gametes occurs in mature ovaries of *A. maura* when water temperatures rise above 25°C, both in the wild (Camacho-Mondragón et al., 2012) and under laboratory conditions (Rodríguez-Jaramillo et al., 2001). In this regard, our samples collected during September (30°C) allowed a detailed ultrastructural characterization of the degeneration process in atretic oocytes. Although the changes recorded in organelles during the oocyte degeneration process in *A. maura* are similar to those observed in other bivalves (Dorange & Le Pennec, 1989; Chung et al., 2008), the degeneration of the oocyte reserves is different. Yolk and lipid granules do not disappear but accumulate to form a dense globular mass in the acinar lumen and cytoplasm of atretic oocytes, as observed in starfishes (Reunov & Crawford, 2010). The presence of large autophagic vacuoles and myelin-like organelles suggests an important degradation activity. This degeneration of oocytes, and their subsequent resorption, allows for the recycling of nutrients to meet the energy demands of basal metabolism (Herlin-Houtteville & Lubet, 1975).

This investigation, which details the different stages of oogenesis and oocyte degeneration, supplements the description of gametogenesis in *A. maura*, which began with an ultrastructural description of spermatogenesis (Camacho-Mondragón et al., 2014). However, a detailed description of specimens undergoing sexual transition is still missing, as it has been reported that this is a protandrous hermaphroditic species (Camacho-Mondragón et al., in press), and an investigation on this aspect would supplement our knowledge of gonad development involving all the sexual conditions known for this species.



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A SURVEY OF THE LAND SNAILS OF KOSRAE (CAROLINE ISLANDS, MICRONESIA) INCLUDING THE REDISCOVERY OF ENDEMIC *DELOS OUALANENSIS* (PEASE, 1866) (MOLLUSCA: PULMONATA: RHYTIDIDAE)

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ABSTRACT

This is the first published documentation of the land snails from Kosrae Island (eastern Caroline Islands, Micronesia; ~ 5.3°N, 163°E). Timed hand collecting in leaf litter and emergent vegetation over the course of five days yielded 15 species in 13 gastropod families, including important collections of *Delos oualanensis* (Rhytididae) and *Sinployea kusaieana* (Charopidae), which had not been collected since the last survey of Kosrae in the 1930s. We did not recover evidence for *in situ* diversification in Kosrae – rather, the fauna seems to be a subset of the general Micronesian fauna (especially that of Pohnpei), with endemic species most likely having sister species off-island. An exotic veronicellid slug, and several snails that are widespread and possibly introduced were found, but no giant African land snails (*Achatina fulica*) were found. Due to its position as the eastern-most high island in Micronesia, Kosrae is an important part of our understanding of both the pre-anthropogenic assembly of Pacific island faunae, and the ongoing homogenization of same. We recommend that future land snail surveys of Kosrae focus on higher elevations and collection methods that preferentially target partulids and leaf-litter microsnails.

Key words: Federated States of Micronesia, Pacific, Oceania, biodiversity, conservation, rainforest.

INTRODUCTION

The vast Pacific region of Micronesia is better known for its coral reefs than tropical rainforests, which might help explain the relative dearth of terrestrial exploration there. The last major, geographically broad Micronesian land snail expedition pre-dated World War II: Bishop Museum's (BPBM; Honolulu, Hawaii) seminal and steamship-powered Micronesian Expedition (19 November 1935 to 2 July 1936; Y. Kondo, unpublished report, 1936), which was facilitated in part by the Imperial Japanese Government and the South Seas Bureau. BPBM's shell collector (and later malacologist and curator) Yoshio Kondo (1910–1990) was the first to conduct comprehensive and systematic land snail surveys of the Caroline Islands, under the mentorship of BPBM founding curator C. Montague Cooke (based in Honolulu, Hawaii). The Caroline Islands include Belau (Republic of Palau) and the island groups that now consti-

tute the Federated States of Micronesia: Yap, Chuuk, Pohnpei and Kosrae (then “Kusaie”; island names follow Motteler (2006)). The Kosrae of the BPBM Micronesian Expedition era, as is the case today, is one of the least well-known Micronesian islands from a land snail faunistic perspective.

The ten days (20 January 1936 to 1 February 1936) spent by Kondo and colleagues on Kosrae were aimed at, for example, “prov[ing] or disprov[ing] the existence of *Partula*” (Y. Kondo, unpublished report, 1936), arguably among the most charismatic large-bodied Pacific land snails, and now also among the most imperiled (Cowie, 1992). Regarding Kosrae *Partula*, Kondo said: “none have been reported since 1830. And no specimens are in any museum” (Y. Kondo, unpublished field notes, Yoshio Kondo Library, BPBM). Kondo succeeded in finding some partulids at several localities, some of which are now represented in the BPBM collections. Evidence that partulids

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were once abundant enough to find them in an expedition lasting only ten days, is significant considering that more than half of the charismatic Pacific-endemic Partulidae are now extinct, and have been particularly hard hit in Micronesia (Cowie, 1992; Pelep & Hadfield, 2011; Ó Foighil & Rundell, 2012).

No published Kosrae land snail survey exists, and few lists exist for other taxa (dragonflies and damselflies: Buden & Paulson 1993; plants: Mueller-Dombois & Fosberg, 1998; ants: Clouse 2007). Therefore, we embarked on a general land snail survey of Kosrae in order to understand the current state of the fauna. Baseline survey efforts are the foundation for solid conservation work and prioritization, which are desperately needed on small islands where forests are central not just to land snail survival, but human livelihoods (e.g., watersheds, food and medicines).

Information on what species are still extant is also the first step in formally assessing the conservation status of species, work that has been done for < 2% of mollusc species (Lydeard et al., 2004). For example, many of Kosrae's indigenous land snail species have never been removed from the IUCN's "Data Deficient" category (e.g., Mollusc Specialist Group, 1996a). Indeed it is not unlikely that Kosrae species could go extinct before their data deficient conservation status is lifted. This is a particular concern for Kosrae endemics, which would not be buffered from extinction by broad geographic distributions. Therefore, families that received special attention in our general survey included Diplommatinidae, Rhytididae, the endodontoid Charopidae (Solem, 1983) and Partulidae, each of which contained Kosrae endemic species previously reported by Kondo in 1936 (Y. Kondo, unpublished field notes, Yoshio Kondo Library, BPBM). Documenting Charopidae and Partulidae was particularly relevant since if rediscovered, they would be among the precious few known populations for these groups in Micronesia, and indeed the Pacific (Lydeard et al., 2004). Similarly, other species (e.g., *Delos oualanensis* (Rhytididae) and undescribed diplommatinids) had not been seen in the wild and documented by a malacologist since 1936. Documenting species localities and habitats, and collecting fresh specimens, is central to future systematic and ecological study of the fauna, and enhances our ability to place Kosrae in a broader geographic and Pacific conservation context.

## MATERIALS AND METHODS

### Geology and Ecology of Kosrae

Kosrae (5.3°N, 163°E) is located approximately 2,000 km northeast of Papua New Guinea, and 4,560 km southeast of Honolulu. It is the Federated States of Micronesia (FSM)'s easternmost island, as well as its smallest (110 km<sup>2</sup>) and least populated state (7,700 people in 2000 and approximately 6,616 in 2010 (FSM Offices of Statistics, Budget and Economic Management, Overseas Development Assistance, and Compact Management). Kosrae's maximum elevation is 629–634 m. Unlike other FSM states, Kosrae lacks numerous satellite islands. The closest high island to Kosrae is Pohnpei, which is 530 km to the northwest.

Geologically, the easternmost islands within the Caroline Islands – such as Kosrae – are distinct from the old and largely limestone Caroline island groups of Belau and Yap to the west (Rundell, 2008). The eastern Caroline high volcanic islands are instead generally regarded as part of a relatively young hotspot island chain ranging in age from 12.4–11.0 million years in Chuuk ("Truk"; 7.5°N, 151°E), to 3.0–7.6 Ma in Pohnpei (6.9°N, 158.2°E) to about 1.0–2.6 Ma in Kosrae (reviewed in Keating et al. 1984). However, Rehman and co-authors (2013) suggested that fracture-induced subduction might have also been involved in eastern Caroline island formation.

Kosrae's lowlands experience a long-term average rainfall of 5.05 m/year (Chimner & Ewel, 2004), but there can be as much as 7.5 m/year in the mountains (Laird, 1983). Swamps are abundant. The main indigenous vegetation types of Kosrae include mangrove, strand, lowland tropical rainforest (most vulnerable to anthropogenic modification, especially for agroforestry), and montane cloud forests (in Kosrae, these begin at approximately 450 m above sea level, which is one of the lowest elevations this pantropical vegetation type occurs at in the world; Gressitt, 1954; Mueller-Dombois & Fosberg, 1998). Like many high volcanic islands in the tropical Pacific, human populations and their impacts are generally most obvious at the coast. The first people to colonize Kosrae likely did so approximately 2,300–2,500 years before present (Ward, 1988). Like other peoples in Micronesia, between the 16<sup>th</sup> and 20<sup>th</sup> centuries, Kosraeans experienced varying levels of colonial rule, first from Spain, then Germany, Japan, and the USA, until FSM independence in 1986.



Survey and Laboratory Methods

Sampling localities are shown in Figure 1 and described in Table 1. The time available for the Kosrae survey was 10 to 15 November 2005. In order to maximize the number of species collected during this time, as well as the potential for finding endemic species, we maximized geographic distance among the ten localities and sought out indigenous forest. We intended to revisit every locality surveyed by Kondo and colleagues in 1936, however, the condition and indigenous forest cover of those historical sites relative to today, in addition to the seasonal difference (i.e., difference in accessibility of higher elevation sites) precluded adherence to this original plan. We arrived in Kosrae during the onset of heaviest rains. However, we did survey many comparable sites, including Lelu or “Lele” Islet (Sta. 102), the type locality for the putative endemic charopid *Sinployea kusaieana* Solem, collected by Kondo (Solem, 1983: 143–145).

Timed collections were made by searching leaf litter and vegetation by hand and by collecting every snail and slug found. Both live and dead shells were collected. Three to four collectors thoroughly searched the leaf litter for 30–60 min (depending on the site) and spent 15 min searching the emergent vegetation at each site, working within the microhabitat patches most likely to yield land snails, based on field experiences elsewhere in Micronesia. Because our survey took place during the rainier season in Kosrae, and was short in duration, some of the highest elevation localities were inaccessible and reaching them in our timeframe was impractical (and would have involved sacrificing the survey’s geographic breadth). We used Kondo’s field notes from 26 January 1936 as a guide: “I thought *Partula*’s liked low altitudes and near rivers and it was quite right.” Furthermore, it made sense to focus on leaf litter, since *Partula* (as well as diplommatinids and charopids; Solem, 1983; Rundell, unpublished data, 2005) would most likely be found in the leaf litter on Kosrae. Kondo stated: “most [Kosrae partulids] were on ground but found two juvs. and one adult on plants” (Y. Kondo, unpublished field notes, Yoshio Kondo Library, BPBM).

Land snail specimens were killed and preserved by submersion in 95% ethanol at the end of each survey day. Ethanol was changed twice subsequently. Field collections were later sorted and identified at the Field Mu-

seum of Natural History (FMNH), BPBM, and SUNY-ESF, using a dissecting microscope. Identifications were made using specimens from the BPBM and Kondo’s unpublished notes and drawings (Yoshio Kondo Library, BPBM). Kosrae collections have been deposited in the FMNH Mollusc Collection (FMNH310579; FMNH 338662–338747). DNA sequences from FMNH310579 (*Palaina* “CC”) are also available on GenBank (accession numbers EU742005, EU742086, EU742046) and published in a phylogenetic context by Rundell (2008).

RESULTS

Species found in the survey (localities in Fig. 1, Table 1) are listed in Table 2. We found 15 species from 13 families. All species are indigenous to Kosrae, with the exceptions of *Subulina octona* (Bruguière, 1792) and *Allopeas clavulinum* (Potiez & Michaud, 1838), which are common tramp species on Pacific islands, but that may have been introduced early in Kosrae’s human history and/or repeatedly thereafter. The juvenile veronicellid species is also a likely human introduction, and also probably a crop pest. No *Achatina fulica* Bowdich, 1822 (also known as *Lissachatina fulica*; Achatinidae), commonly introduced

TABLE 1. Geographic coordinates for Kosrae collection localities.

| Station | Latitude (°E) | Longitude (°N) | Notes                          |
|---------|---------------|----------------|--------------------------------|
| 102     | 5.3306        | 163.0294       | Lelu Islet                     |
| 103     | 5.2842        | 162.9572       | Sipyen Falls, Sipyen, Utwe     |
| 104     | 5.3095        | 162.9218       | Walung                         |
| 106     | 5.3352        | 162.9760       | Uket, Tafunsak Municipality    |
| 107     | 5.3428        | 162.9599       | Finoluf, Tafunsak              |
| 108     | 5.3012        | 163.0310       | Beach near Point Lejeune       |
| 109     | 5.2926        | 163.0129       | Omma (Malem), up mountain      |
| 110     | 5.2913        | 163.0127       | Omma (Malem), further up slope |
| 111     | 5.3280        | 162.9980       | Innem                          |
| 112     | 5.3622        | 163.0087       | Bikusrik                       |



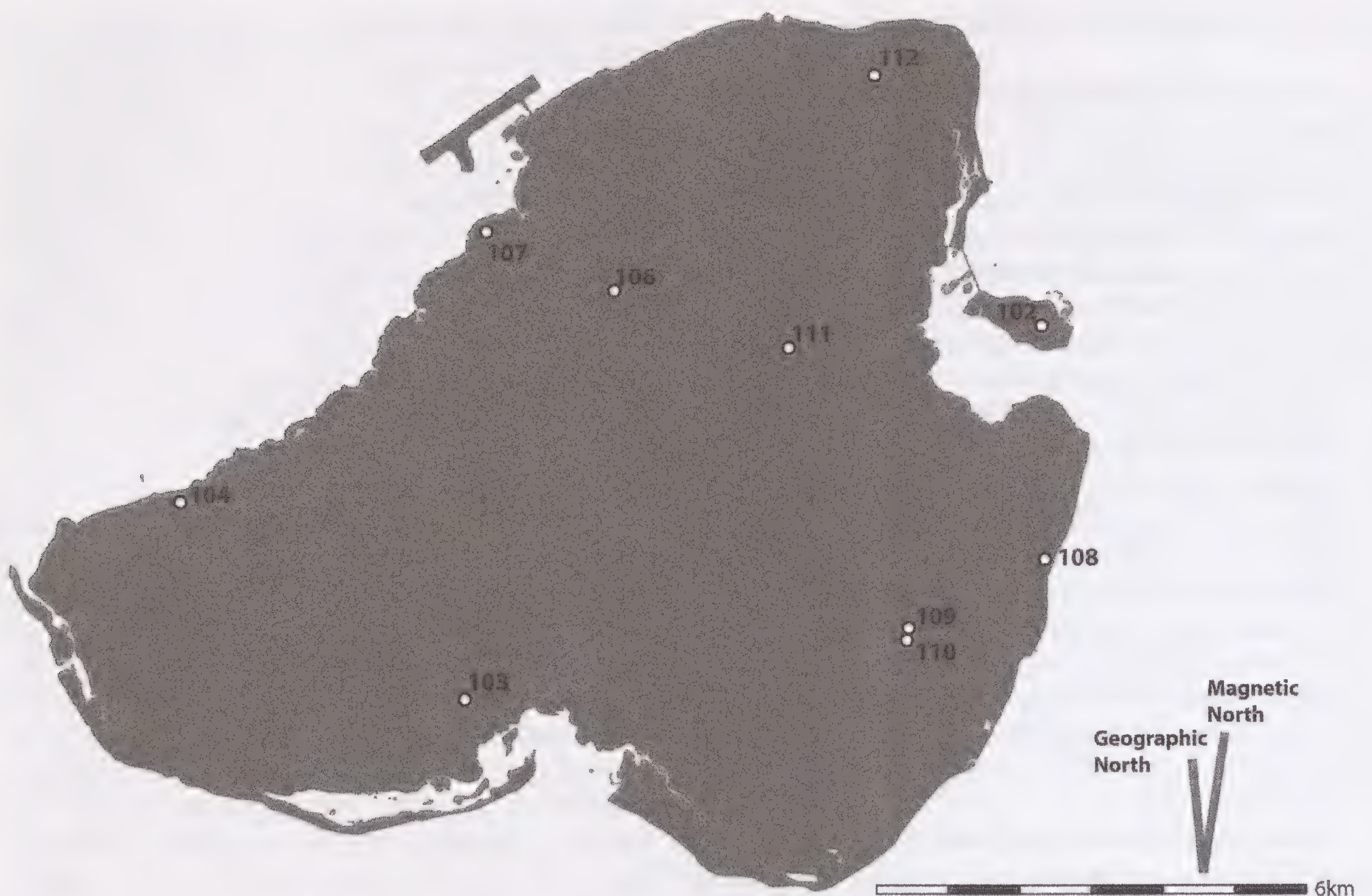


FIG. 1. The Island of Kosrae (Caroline Islands, Micronesia) and survey localities (modified from the USGS map of Kosrae: NGA 6737 II NE-series W856).

crop pests, were found or collected; however in the past they had been informally noted in a localized (and subsequently thwarted) outbreak adjacent to the Kosrae Island Resource Management Authority (KIRMA) facility (Rundell, unpublished data, 2005).

No partulids (e.g., *Partula martensiana* Pilsbry, 1909) were found, but a charopid (*Sinployea kusaieana* Solem, 1983) and a pupillid were collected. The *S. kusaieana* collection represents a new locality for the species. It was not collected in either locality reported by Solem (1983), that is Sta. 102, 104 (Fig. 1). A single undescribed species of diplommatinid, likely endemic to Kosrae (Rundell, 2008; Y. Kondo, unpublished report, 1936; Rundell, unpublished data, 2005), was collected at a few localities (Table 2). This species is informally designated as *Palaina* "CC" pending description (Rundell, 2008) and corresponds to Kondo's unpublished notes and illustration of *Palaina* "N" "Kusaie" (Y. Kondo Library, BPBM). Four other undescribed species were collected: a hydrobiid, a pupinid, and two achatinellids. Although species in these families are notoriously difficult to identify

and distinguish from congeners, comparative material from the BPBM supports their unique identities. The helicarionid species cf. *Kororia palaensis* (Semper, 1870) (based on preliminary conchological and molecular evidence) was found in the greatest abundance of any putative indigenous species found.

One of the most interesting finds was *Delos oualanensis* (Rhytididae), which had not been reported in Micronesia since Kondo's collection in 1936 (Y. Kondo, unpublished report, 1936). Although it was found alive in very low abundance, we collected it at four of the ten localities.

## CONCLUSIONS

Kondo reported 24 species from eleven families in 1936. We found 15 species from 13 families in 2005. Some of Kondo's reported species might represent taxonomic over-splitting (e.g., he reported five subulinid species), but additional morphological study is needed to confirm this. At least for the diplommatinids, we



know that based on Kondo's illustrations and his unpublished descriptions of three putative species, that at least two of these are good species, likely Kosrae endemics, yet we found only one during this survey. Added to the reduced species diversity found in this survey are the unfortunate discoveries of a veronicellid slug and two common tramp species of subulinids. Taken together these findings are evidence of

homogenization of the Kosrae land snail fauna, a phenomenon that is increasingly common across the entire Pacific (Cowie, 2001a).

It should be noted that our surveying techniques were adequate in Kosrae, and elsewhere in Micronesia, to find diplommatinid land snails ranging in size from 3–8 mm (indeed, diplommatinids were target taxa for the survey, see e.g., Rundell 2008), a charopid and a

TABLE 2. Species collected at each Kosrae locality. Pulmonates begin with Ellobiidae. Species labeled "sp. 1" or "CC" are undescribed species. Refer to Figure 1 for map of localities and Table 1 for geographic coordinates.

| Species                                                   | 102 | 103 | 104 | 106 | 107 | 108 | 109 | 110 | 111 | 112 |
|-----------------------------------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Assimineidae                                              |     |     |     |     |     |     |     |     |     |     |
| <i>Omphalotropis laevis</i> (Pease, 1865)                 |     |     | +   | +   |     |     |     |     | +   | +   |
| Diplommatinidae                                           |     |     |     |     |     |     |     |     |     |     |
| <i>Palaina</i> sp. "CC"                                   |     |     |     |     | +   |     | +   | +   | +   | +   |
| Helicinidae                                               |     |     |     |     |     |     |     |     |     |     |
| <i>Pleuropoma zonata</i> (Lesson, 1831)                   | +   | +   |     |     |     |     | +   | +   | +   | +   |
| Hydrobiidae                                               |     |     |     |     |     |     |     |     |     |     |
| hydrobiid sp. 1                                           | +   |     |     |     |     |     | +   |     |     |     |
| Pupinidae                                                 |     |     |     |     |     |     |     |     |     |     |
| <i>Pupina</i> sp. 1                                       |     | +   |     |     |     |     | +   | +   | +   | +   |
| Achatinellidae                                            |     |     |     |     |     |     |     |     |     |     |
| achatinellid sp. 1                                        |     |     |     |     |     |     |     |     |     | +   |
| achatinellid sp. 2                                        |     |     |     |     |     |     |     |     |     | +   |
| Charopidae                                                |     |     |     |     |     |     |     |     |     |     |
| <i>Sinployea kusaieana</i> Solem, 1983                    |     |     |     |     |     |     |     |     | +   |     |
| Ellobiidae                                                |     |     |     |     |     |     |     |     |     |     |
| <i>Melampus</i> cf. <i>luteus</i><br>Quoy & Gaimard, 1832 |     |     |     |     |     | +   |     |     |     |     |
| Helicarionidae                                            |     |     |     |     |     |     |     |     |     |     |
| cf. <i>Kororia palaensis</i> (Semper, 1870)               | +   | +   |     | +   | +   |     | +   | +   | +   | +   |
| Pupillidae                                                |     |     |     |     |     |     |     |     |     |     |
| pupillid sp. 1                                            |     |     |     |     |     |     |     |     |     | +   |
| Rhytididae                                                |     |     |     |     |     |     |     |     |     |     |
| <i>Delos oualanensis</i> (Pease, 1866)                    | +   |     |     |     | +   |     | +   | +   | +   | +   |
| Subulinidae                                               |     |     |     |     |     |     |     |     |     |     |
| <i>Allopeas clavulinum</i><br>(Potiez & Michaud, 1838)    | +   | +   | +   |     | +   |     | +   | +   | +   | +   |
| <i>Subulina octona</i> (Bruguière, 1792)                  | +   | +   | +   | +   | +   |     | +   | +   | +   | +   |
| Veronicellidae                                            |     |     |     |     |     |     |     |     |     |     |
| veronicellid sp. juv.                                     | +   | +   |     | +   |     |     | +   | +   | +   | +   |



pupillid. However, it is likely that additional collection methods (especially microscope-aided leaf litter sieving) across a larger elevation gradient would yield additional species. As with almost all other Pacific islands, the extent of indigenous lowland rainforest in Kosrae has decreased since the BPBM's Micronesian Expedition. Whitesell and coworkers (1986) reported a net increase from 16.5% to 23.1% of the total land area of Kosrae being covered in agroforest between 1975 and 1983; the overall trend of habitat conversion is likely to at least partially account for the reduced species diversity discovered during our survey (Lydeard et al., 2004). Our five days' field work, given reduced forest cover in the lowlands, could therefore be considered comparable to Kondo's efforts, since he claimed, "Insects and shells are so scarce [on Kosrae] that a suitable survey was made in ten days' collecting" (Y. Kondo, unpublished report, 1936). We also note that decreased land snail diversity in itself can be used as an indicator of anthropogenic disturbance (Douglas et al., 2013).

Perhaps most disappointing was the lack of *Partula martensiana* in our survey of Kosrae. Kondo reported *P. martensiana* in 1936 (Y. Kondo, unpublished data). *Partula martensiana* is listed as CR A1ce+2e "in need of updating" by the IUCN. Although our study is not definitive evidence that *P. martensiana* is now extinct, it is not unlikely that if it is extant that it is now exceedingly rare. It is possible that searches at higher elevations could yield partulids, as is the case for other Pacific snails that survive only in high ridge refugia (Lydeard et al., 2004). However, Kondo's notes (unpublished, 1936) that *Partula* was more common at lower elevations near rivers suggests that *P. martensiana* may have been extirpated precisely because of this lower elevation, ground-dwelling habitat preference and therefore higher elevation individuals might not be recovered. The decline and potential extinction of partulid species has been repeated throughout the Pacific and unfortunately our data point in this direction for Kosrae as well.

Despite recent insights on the Kosrae land snail fauna's conservation status, it is still worthwhile to make comparisons with patterns of endemism in other known Kosrae taxa. Odonates, plants and ants reveal a general trend of being a subset of the biota of Pohnpei, with low rates of endemism (Buden & Paulson 1993; Mueller-Dombois & Fosberg, 1998; Clouse 2007). Although more study of both

Pohnpei's and Kosrae's land snails is needed, particularly from a taxonomic perspective (e.g., undescribed species remain at the BPBM, and most groups are in dire need of taxonomic revision), the number of undescribed, endemic species found in this study (and by Kondo) relative to the total number collected indicates that although Kosrae's fauna is relatively small, there may be higher rates of endemism, and even single-island sister species (e.g., within Diplommatinidae or Pupillidae). Still there are other species whose distributions remain a puzzle. For example, Cowie et al. (1996) note that *Kororia palaensis* may occur on multiple Pacific islands and may have been spread by human activities, although it deserves additional taxonomic study. Its tentative geographic distribution (Table 2), and our results support this, however we cannot speculate as to how it might have moved around Micronesia.

Our recommendations for conservation managers are twofold. First, there are still interesting indigenous and endemic land snail species on Kosrae that are both worthy of protection and that could be potentially developed as indicators of forest health. Among these species are *Delos oualanensis*, which is a small but beautiful tiger-striped snail that also represents an entire evolutionary lineage of snails that is uncommon in Micronesia. Its name derives from "Oualan," a historical word for Kosrae (Kondo, 1943). Kondo (1943) suggested that there are two co-occurring forms of this species. *Delos oualanensis* is still listed as Data Deficient by the IUCN (Mollusc Specialist Group, 1996c). The undescribed *Palaina* species, *Sinployea kusaiana*, and *Omphalotropis laevis* (Pease, 1865) are notable. Searches for partulids should continue, and these land snails are the most likely to be spotted by laypersons since they are relatively large-bodied and sometimes may occur on emergent vegetation. Above all, forest land snails like these need forest. Land snails may also provide important calcium sources for indigenous nesting birds (Graveland, 1996).

Second, prevention of introduction of non-indigenous species is paramount. Introduced pest snails and slugs often arrive as eggs in soil or attached to imported vegetation, which can be easily carried around the island and thus quickly spread. Growing native crops and avoiding imported plants for ornamental use can help decrease the risk of introducing potentially devastating pests such as slugs. Currently, to our knowledge, Kosrae still lacks



*Achatina fulica* and according to Gressitt (1954), *Achatina* had not been introduced to the islands by the early 1950s. Because this crop pest snail occurs throughout the Pacific it is not unlikely that a visitor could inadvertently introduce it, or that a fertile snail or its eggs could arrive from another Pacific island in luggage or cargo. It is advised that any detected outbreaks of *A. fulica* or other mollusc pests be dealt with immediately by hand picking and freezing or drowning, but that biocontrol methods such as the widely introduced snail *Euglandina rosea* (Férussac, 1821) or the flatworm *Platydemus manokwari* de Beauchamp, 1963, are not employed to combat introduced *A. fulica* (Cowie, 2001b). This is because these predators have been shown to be ineffective in controlling *A. fulica* but are deadly to remaining indigenous Pacific land snail species (Clarke et al., 1984; Hadfield et al., 1993; Lydeard et al., 2004). These indigenous and endemic land snails are a treasure to Kosrae and the Federated States of Micronesia.

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SHELL AND GENITAL MORPHOLOGY FAILS TO SEPARATE  
*ANCOTREMA HYBRIDUM* (ANCEY, 1888) AND *A. SPORTELLA* (GOULD, 1846)  
(GASTROPODA: HAPLOTREMATIDAE)

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ABSTRACT

The obsolescence of radial sculpture on the last whorl of the land snail *Ancotrema hybridum* (Ancey, 1888) has been used to separate it from *A. sportella* (Gould, 1846), but shells are sometimes difficult to assign to one species or the other, prompting questions about their species status. Factor analysis of shell characters of 311 specimens of *Ancotrema* Baker, 1931, including characters of surface sculpture strength, shell size and rib density, revealed continuous variation of these characters without bimodality. Radial sculpture begins obsolescing at about whorl five, so shells that stopped growing near whorl five have *A. sportella*-like morphology, while those that continued growing after whorl five have *A. hybridum*-like morphology. We saw no meaningful differences in the genital anatomy that would suggest different species. The obsolescence of sculpture beginning about whorl five regardless of ultimate whorl number, lack of bimodality of shell characters, and lack of anatomical differences lead us to conclude that the two forms are a single species. *Ancotrema hybridum* is a junior synonym of *A. sportella*.

Key words: *Haplotrema*, identification, land snail, morphology, ontogeny, surface sculpture.

INTRODUCTION

The omnivorous land snails in the family Haplotrematidae (whose diet includes other snails) have their greatest diversity along the west coast of North America (Pilsbry, 1946; Schileyko, 2000) where 14–16 of the 16–18 species (Turgeon et al., 1998; Roth & Sadeghian, 2003) in North America (north of Mexico) occur. The two genera into which these species have been classified, *Haplotrema* Ancey, 1881, and *Ancotrema* Baker, 1931, are separable on anatomical features and by the presence of coarse spiral striae cutting the tops of the radial ribbing in *Ancotrema* (Roth, 1991) yielding a beaded sculpture. While most of the species of the continental North American Haplotrematidae are readily identifiable, some individual specimens of *A. sportella* (Gould, 1846) and *A. hybridum* (Ancey, 1888) are difficult to assign, calling into question whether they are indeed separate species.

Since the time the form *Ancotrema hybridum* was recognized, its status has changed from a sub-taxon of *A. sportella* to its being considered

a full species. Previously, *Ancotrema* as currently recognized was considered a section (Pilsbry, 1946) within *Haplotrema* with *Helix sportella* as its type species. Gould (1846) gave the habitat of *A. sportella* as “Puget Sound, Oregon,” thus fixing the type locality. (Puget Sound was located in Oregon Territory until the formation of Washington Territory in 1853.) Gould’s holotype for *A. sportella* is at the United States National Museum (USNM 5442) (Johnson, 1964; Roth & Sadeghian, 2003), but our examination of that specimen showed it to be immature and lacking features necessary to distinguish *A. sportella* and *A. hybridum*, with consequent uncertainty whether it actually represents the form *A. sportella* or *A. hybridum*. Whether or not paratype 169376 at Museum of Comparative Zoology (Johnson, 1964) is adult or immature is irrelevant as the holotype is the name bearer.

Pilsbry (1946) recognized *Ancotrema sportella hybridum* as subspecifically distinct from *A. sportella sportella* by having reduced sculpture on most or all of the last whorl in the former. Roth (1990) elevated *Ancotrema* to full genus, named a new species, and recognized four

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species in the genus. Subsequent authors, including Turgeon et al. (1998), have continued to use *Ancotrema* as a genus, although Schileyko (2000) used it as a subgenus in *Haplotrema*. Roth (1990) elevated *A. hybridum* to specific rank, and Roth (1991) continued to consider *A. hybridum* and *A. sportella* to be specifically distinct and designated a lectotype for *A. hybridum* (Santa Barbara Museum of Natural History [SBMNH] 35134 from Astoria, Oregon). Roth (1991: 159) reiterated that the two forms are separable by the "obsolescence of radial ribs on the penult and body whorls" of *A. hybridum*.

Roth (1990, 1991) reported that *Ancotrema hybridum* and *A. sportella* occur sympatrically over much of their range without intergradation, in some cases at the same localities. However, Roth (1991) acknowledged Baker's (1931) report of intergradation between *A. hybridum semidecussatum* Gratacap, 1901, and *A. sportella* in western Washington. The geographical ranges of *A. hybridum* and *A. sportella* reported by Roth & Sadeghian (2003) coincide, from northern California to the Aleutian Islands, Alaska.

Although Roth (1991) considered *Macrocyclis vancouverensis* var. *semidecussatum* to be an unavailable name because the original publication reported a name on a collection label and the author did not intend to propose a new

taxon, we hold that Gratacap (1901) satisfied the requirements for availability. He named and described the specimen, and although he expressed the possibility, he did not explicitly state that it was a junior synonym (ICZN Code, 1999: Article 11.6). Nevertheless, we agree with Pilsbry (1946) and Roth (1991) that *Ancotrema semidecussatum* is a junior synonym of *A. hybridum* and is unrelated to *Haplotrema vancouverensis* (Lea, 1839).

That some specimens are difficult to assign to species, and that their ranges coincide geographically, led us to question whether *Ancotrema sportella* and *A. hybridum* are separate species. To address this question, we examined 311 shells of *Ancotrema*, focusing on the shell characters previously recognized as important for separating the taxa. If the taxa were separate species, we expected to see bimodality in at least some of the features, especially in features that have been used for separating the species in the past. We compared dissected genital anatomies of five *A. hybridum* and four *A. sportella*, with a published drawing of *A. sportella* anatomy.

In this paper, we demonstrate a lack of bimodality in the morphometric characters and lack of major differences in genital anatomies, suggesting that the two forms are a single species.

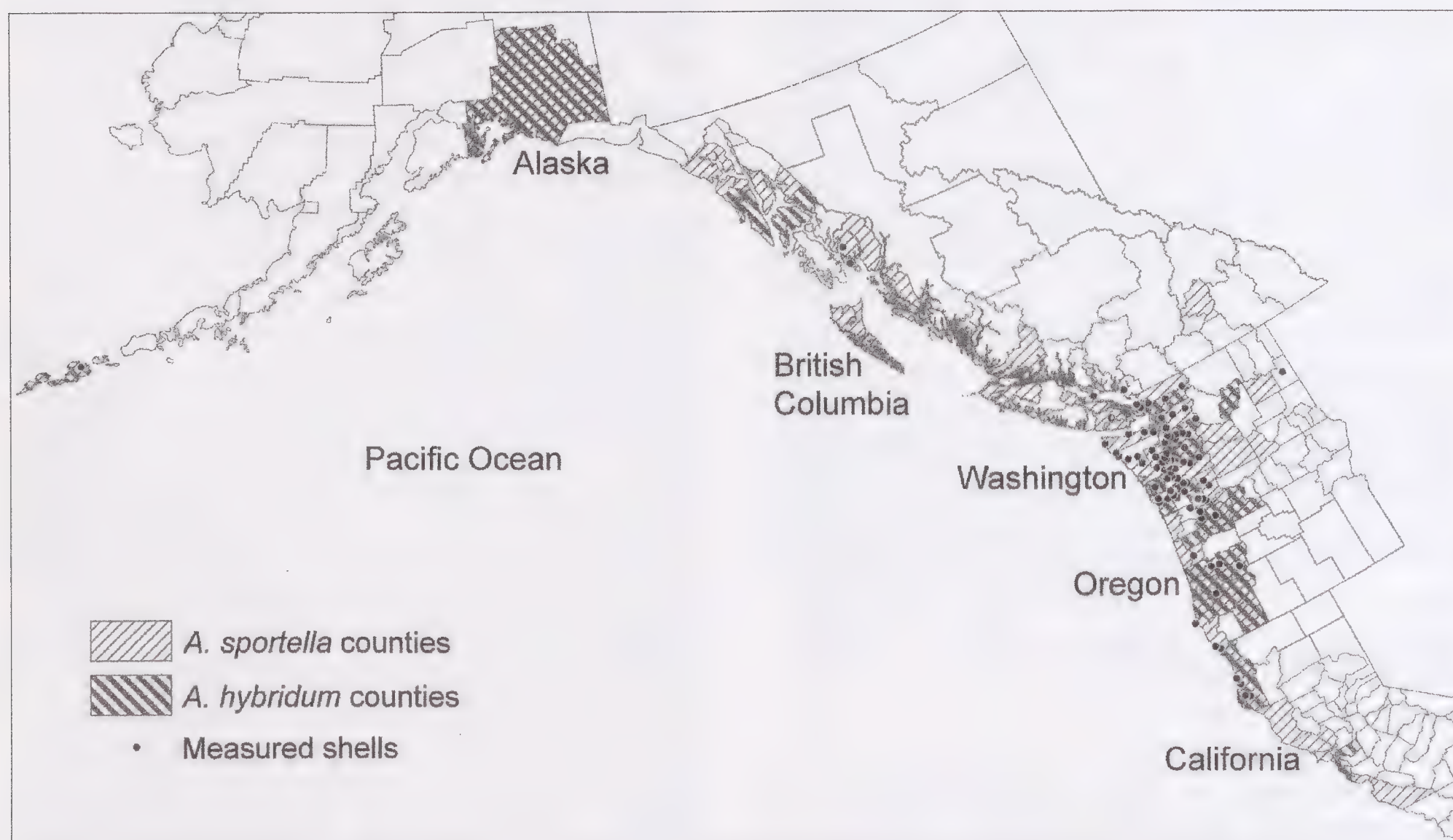


FIG. 1. Map showing historically known occurrences in counties or county equivalents of the two forms of *Ancotrema* (shading), and indicating sample origins of the measured specimens (dots).



# MATERIALS AND METHODS

## Shell Morphometry

We examined 311 adult specimens (adults are recognizable by modification of the peristome including downward deflection of the dorsal margin) of *Ancotrema* from the research collection at Carnegie Museum of Natural History [CM] and the lectotype of *A. hybridum* from SBMNH. Some of the CM specimens had been previously identified as *A. sportella*, others as *A. hybridum*, and some were simply identified as *Ancotrema* sp. without certain identity.

The map in Figure 1 shows the historically known ranges of the two forms, using dots to indicate the origins of the specimens we measured. While most measured specimens are from the Washington and Oregon sections of the ranges, some measured specimens are from the California, British Columbia and Alaska sections of the ranges. Historical information on range was obtained from the follow-

ing museums: Academy of Natural Sciences, Carnegie Museum [CM], Florida Museum of Natural History, Field Museum of Natural History, Museum of Comparative Zoology, Santa Barbara Museum of Natural History [SBMNH], University of Michigan Museum of Zoology and University of Washington Burke Museum. Historical information is reported at the level of county or county equivalents.

We selected characters (Fig. 2): diameter (D); whorls (W) (by the method of Burch, 1962: 15; counted to the inside margin of the last whorl, to the nearest 0.05 whorls); rib density (RD) (linear distance occupied by four rib wavelengths or a line spanning five ridge tops, at inner edge of whorl four, converted to ribs per mm, average of three measures at adjacent positions along the whorl); whorl number where obsolescence of radial ribs begins (WNOB) (rib strength evaluated relative to strength on adjacent previous whorl); whorls back from aperture where beaded sculpture weakens (WBBW) (relative to strength on adjacent pre-

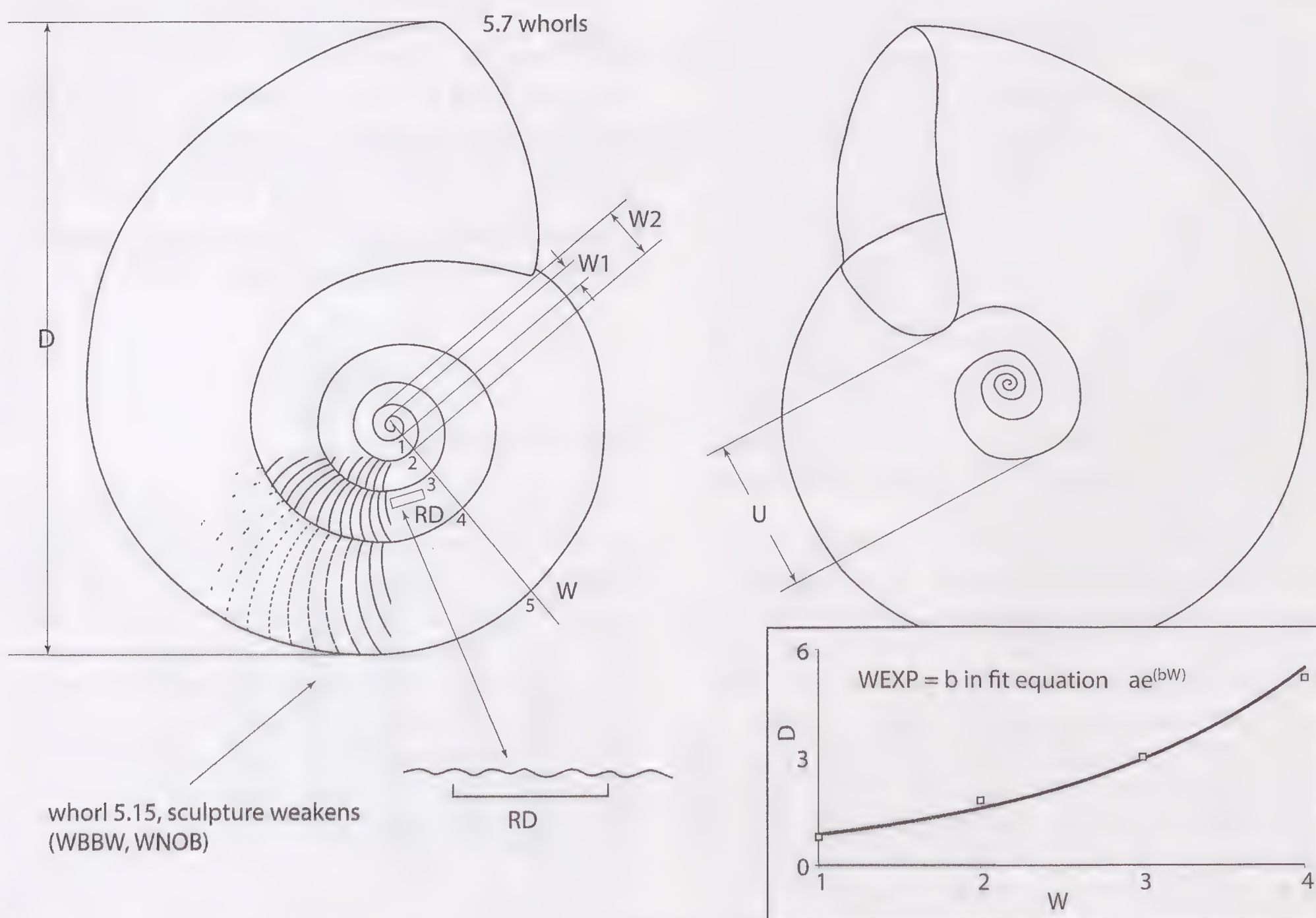


FIG. 2. Characters measured on *Ancotrema* specimens. Abbreviations: WBBW – whorls back from aperture where beaded sculpture weakens, D – diameter, RD – rib density (ribs per mm), U – umbilical diameter, W – whorls, W1 – diameter of whorl 1.0, WEXP – whorl expansion rate, WNOB – whorl number where rib obsolescence begins.



vious whorl); umbilical diameter (U), diameter of whorl 1.0 (W1) (to the nearest 0.02 mm); and whorl expansion rate (WEXP) (calculated from best fitting exponential curve of suture to suture diameters at whorls 1, 2, 3, and 4, using Microsoft Excel, expressed as coefficient  $b$  from the equation, diameter =  $ae^{(bW)}$ ).

The point at which radial ribs and beaded sculpture weakened was subjectively estimated with respect to the strength of the sculpture on the adjacent previous whorl. In practice, the observer could locate a point later in growth at which the sculpture was clearly weaker, and a point earlier in growth at which the sculpture was approximately the same strength as the previous whorl. To score WNOB, we selected a point midway between those extremes and considered that to be the point at which the sculpture began to weaken. The same approach was followed for scoring WBBW. In most shells, the two extremes were a few tenths of a whorl to less than a half whorl apart, so reproducibility should be less than that amount.

Although Baker (1931) conceived *A. sportella* to be a smaller form (< 18 mm diameter) occurring in the Puget Sound area and *A. hybridum* to be a larger (> 18 mm) more widespread form, the main character given by Pilsbry (1946) and Roth (1991) for separating the two forms is obsolescence of the radial ribs on the last whorl. Consequently, we closely examined both size and obsolescence of sculpture. To score shells for rib obsolescence, we interpreted obsolescence to mean decrease in cross sectional amplitude of ribs, relative to the strength on the adjacent previous whorl. We included rib density as a character in the analysis because a preliminary examination of a dozen shells of each form suggested a possible difference between forms in rib density.

In order to examine how the two forms separated in morphological space, we assigned individual shells to one or the other species, and left some as unidentified. In some individuals, the rib strength diminished relatively far back from the aperture edge (so they were like *A. hybridum*), while in other individuals the rib strength remained strong to the end of growth (so they were like *A. sportella*). However, the rib strength of many individuals diminished a distance back from the aperture edge that was intermediate between these two extremes, so those specimens were difficult to classify. We used the following criteria to assign specimens to species objectively: rib strength diminished  $\leq 0.25$  whorls behind aperture

edge as *A. sportella*, 0.25–0.75 whorls behind as unidentified, and those  $\geq 0.75$  behind as *A. hybridum*.

We performed Factor Analysis on these eight variables using varimax rotation in Systat 10 (Systat, 2000).

## Anatomy

In order to explore whether the two forms show internal anatomy differences, we dissected individuals of the two forms and compared distal genitalia. Reasoning that individuals showing the greatest differences in shell morphometry have the best chance of showing anatomical differences, we selected individuals that plotted toward the extremes on preliminary shell morphometric factor analysis plots. We dissected four specimens identified as *Ancotrema sportella* (CM80145A, CM80145B, both from King Co., Washington; CM80208C, Lane Co., Oregon; CM121319, Snohomish Co., Washington) and five as *A. hybridum* (CM64881G, Lewis Co., Washington; CM80207, Lane Co., Oregon; CM80422, Wahkiakum Co., Washington; CM121320, Clatsop Co., Oregon; CM132741, Multnomah Co., Oregon). One of the *A. sportella* (CM80145B) we dissected appeared to be immature or to have an undeveloped male side, so its anatomy is not considered in detail in this paper. We compared anatomies to a published anatomy drawing of *A. sportella* (Pilsbry, 1946).

## RESULTS

### Shell Morphometry

The distinguishing features recognized for separating these two forms (Baker, 1931; Pilsbry, 1946; Roth, 1991) is shell size and obsolescence of radial ribs on the final whorls. If the two forms are separate species, some features might be expected to show bimodality. Bimodality of size was not evidenced in a graph showing the relationship between two of the most obvious features in snail shells, number of whorls and diameter (Fig. 3;  $r^2 = 0.6558$ ,  $n = 226$ ,  $P < 0.001$ ). Furthermore, a histogram showing the number of whorls back from the aperture where the radial ribs weakened demonstrated continuous variation as opposed to bimodality, although the graph does show a positively skewed tail (Fig. 4). Therefore, if they were separate species, obsolescence of radial



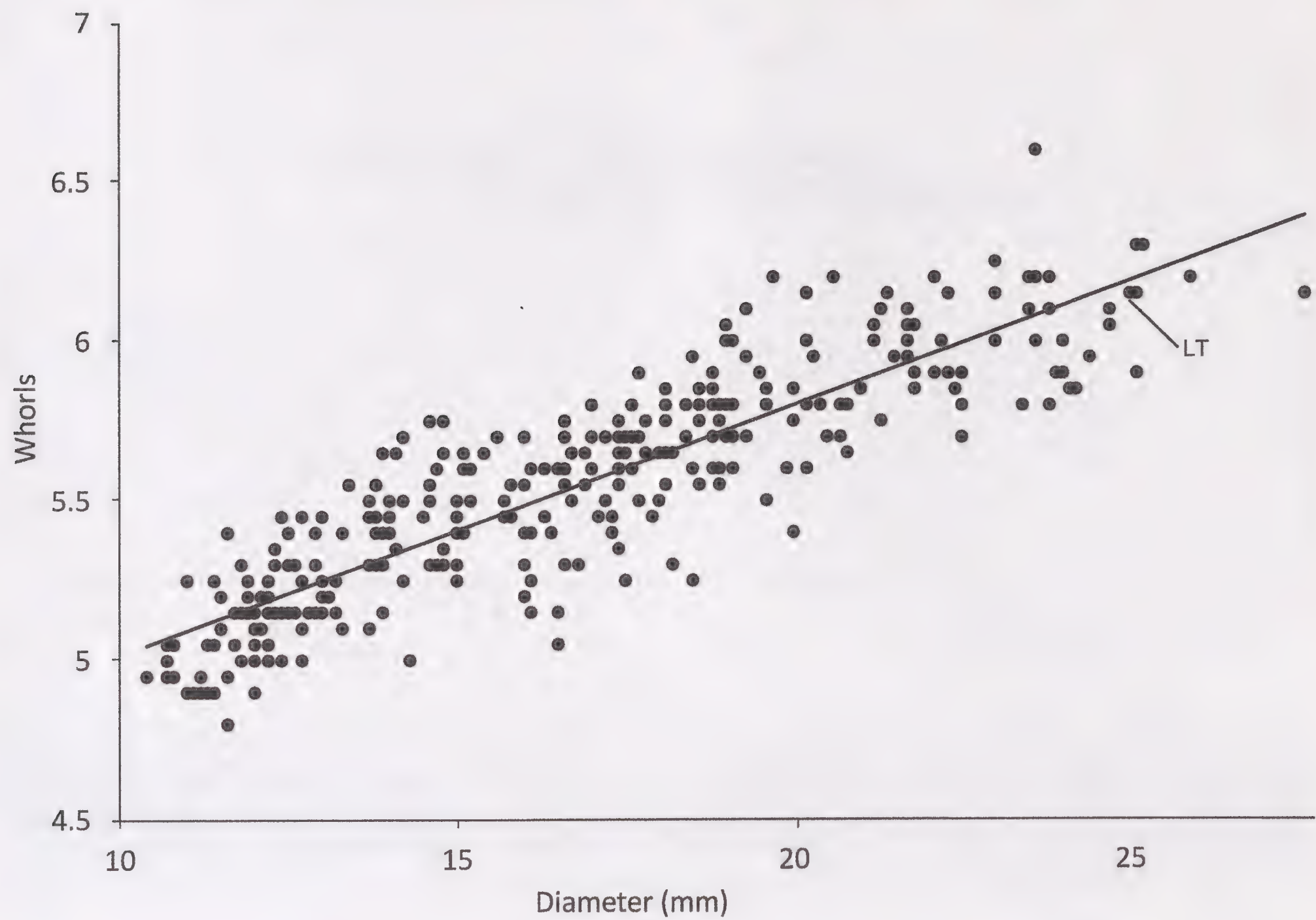


FIG. 3. The relationship between whorl number and shell diameter in *Ancotrema*. ( $R^2 = 0.7796$ ,  $n = 312$ ,  $p < 0.001$ ). Lectotype of *A. hybridum* indicated (LT).

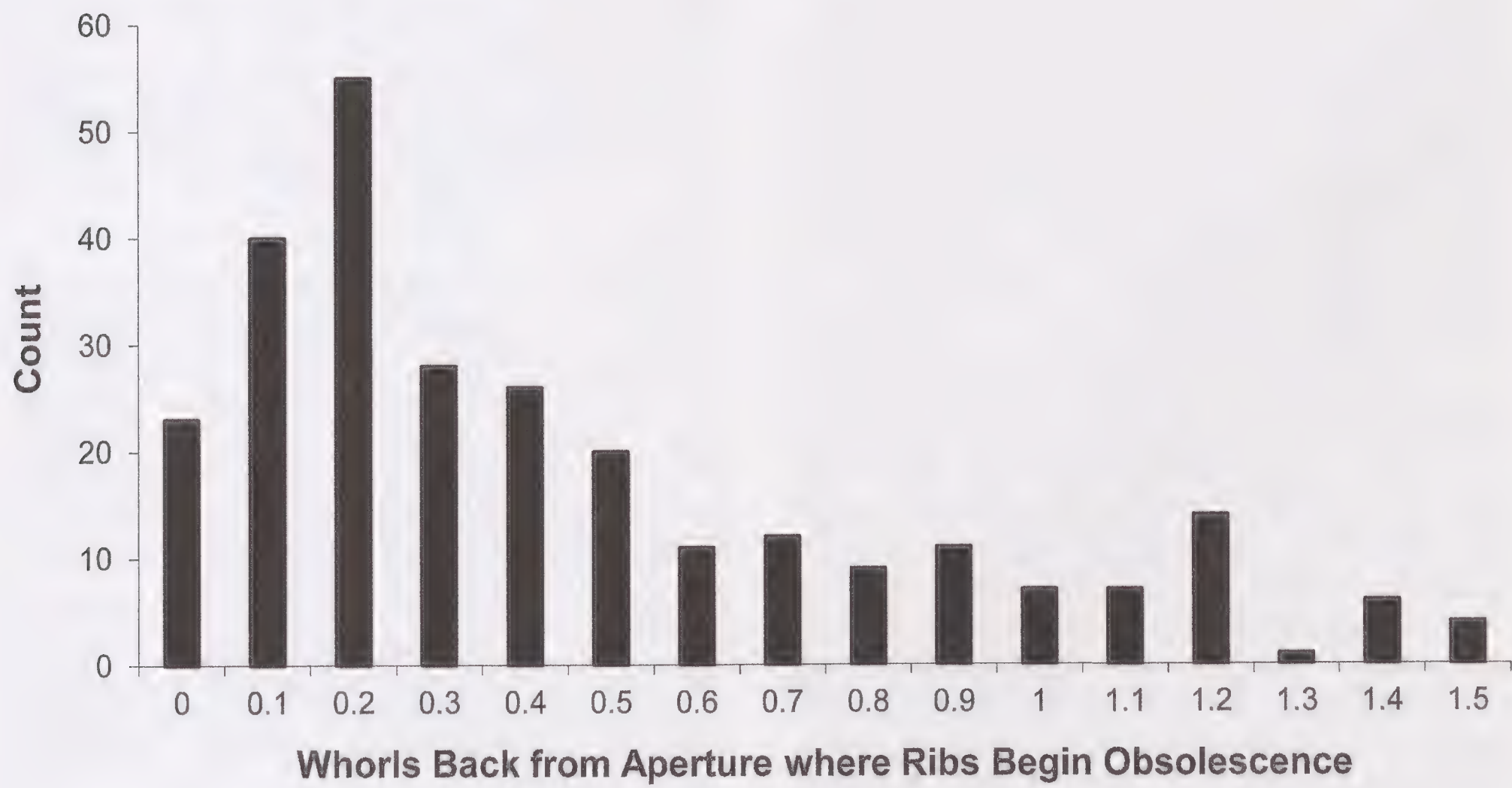


FIG. 4. Histogram showing numbers of individuals for which the radial sculpture weakened at various numbers of whorls back from the aperture.



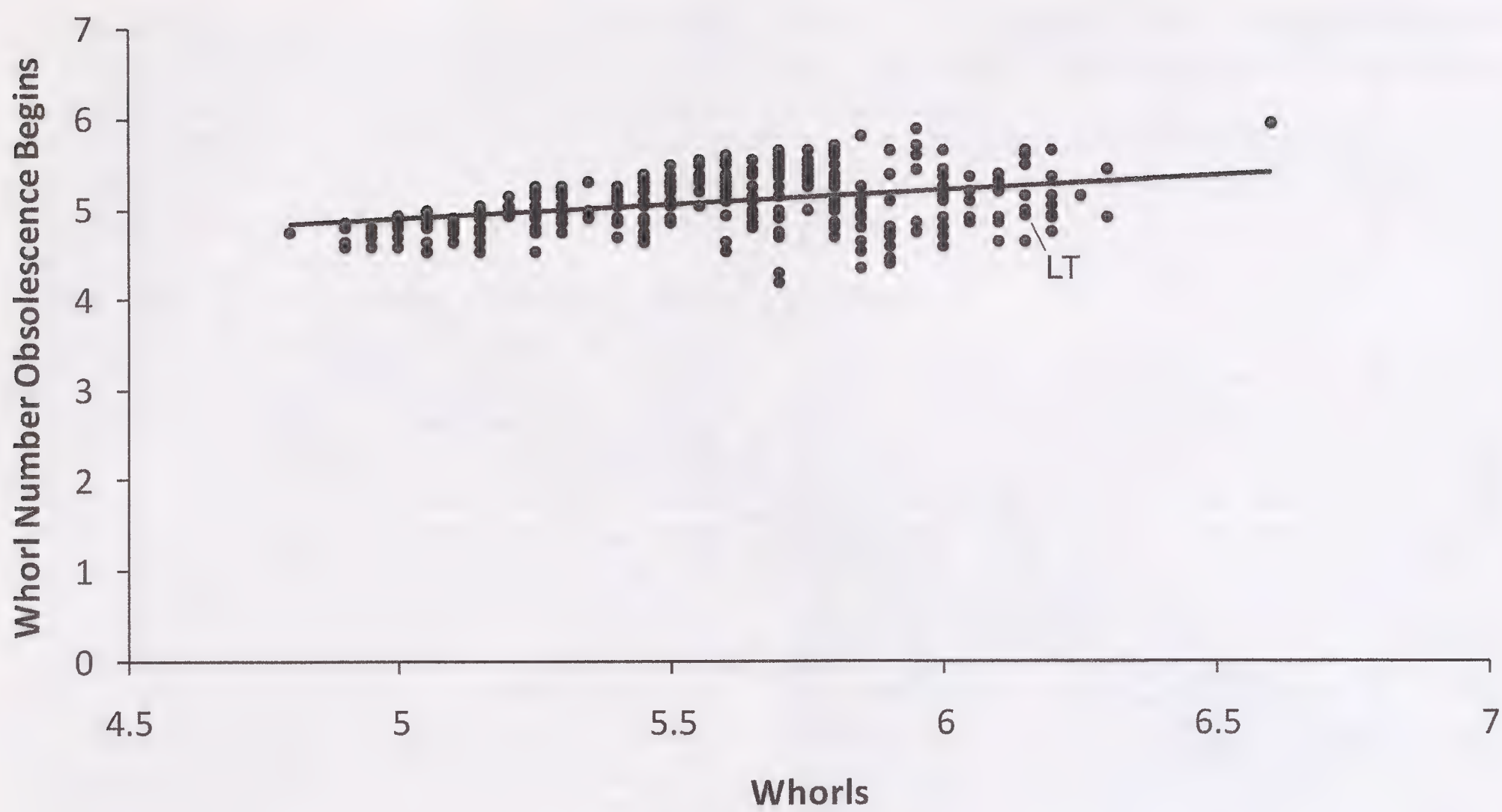


FIG. 5. Whorl Number at which rib Obsolence Begins (WNOB) plotted by whorls. Start of rib obsolescence is independent of whorl number ( $R^2 = 0.1098$ ,  $n = 274$ ,  $0.1 > p > 0.05$ ), although adult shells with more whorls tend to begin rib obsolescence at slightly greater whorl numbers ( $y = 0.2905x + 3.414$ ). Lectotype of *A. hybridum* indicated (LT).

ribs on the final whorl does not seem to be a useful feature for distinguishing them.

Obsolescence of radial ribs began at about whorl number five on all specimens regardless of the number of whorls in the shell (Fig. 5). Before whorl five, radial sculpture was generally strong, while after five whorls, radial sculpture had generally weakened. Interestingly, the point at which rib obsolescence begins occurs at slightly larger whorl sizes in larger shells (about 0.3 whorl later per whorl larger,  $r = 0.347$ , d.f. 311,  $p < 0.001$ ). Although the increase is statistically significant, it is a shallow slope.

Rib density showed continuous variation (in contrast to preliminary analysis suggesting a difference between the two forms). Mean rib density measured at the inner edge of whorl four ranged from 4.58 to 12.64 ribs per mm (mean 7.25) and the factor analysis showed that more *A. hybridum*-like shells had more ribs per mm.

In the factor analysis, the first three eigenvalues explained 42, 20, and 18% of the variance, respectively (Table 1). Three size variables, diameter (D), whorls (W), and umbilicus (U) loaded strongly on factor 1, with moderate loading of number of whorls back at which the beaded sculpture weakens (WBBW). Whorl number at

TABLE 1. Loadings for the eight variables on the three factors from factor analysis of 311 specimens of *Ancotrema*, using the rotated factor method. Bold loadings indicate the main variables loading on each factor. Percent variance explained is after varimax rotation. Abbreviations: D – shell diameter; W – whorls; U – umbilical diameter; WBBW – whorls back from aperture where beaded sculpture weakens; WNOB – whorl number at which obsolescence of ribs begins; RD – rib density; W1 – diameter of whorl 1.0; WEXP – whorl expansion rate.

|                        | Factor 1       | Factor 2        | Factor 3        |
|------------------------|----------------|-----------------|-----------------|
| D                      | <b>0.97134</b> | 0.08645         | -0.00296        |
| W                      | <b>0.95442</b> | -0.08065        | 0.05083         |
| U                      | <b>0.95767</b> | 0.04301         | -0.01262        |
| WBBW                   | <b>0.67431</b> | <b>0.62276</b>  | 0.04891         |
| WNOB                   | 0.26767        | <b>-0.87601</b> | 0.04777         |
| RD                     | -0.19344       | <b>-0.66870</b> | 0.02744         |
| W1                     | 0.06653        | 0.08783         | <b>-0.85872</b> |
| WEXP                   | 0.09372        | 0.03400         | <b>0.83834</b>  |
| Variance explained (%) | 41.9           | 20.3            | 18.1            |



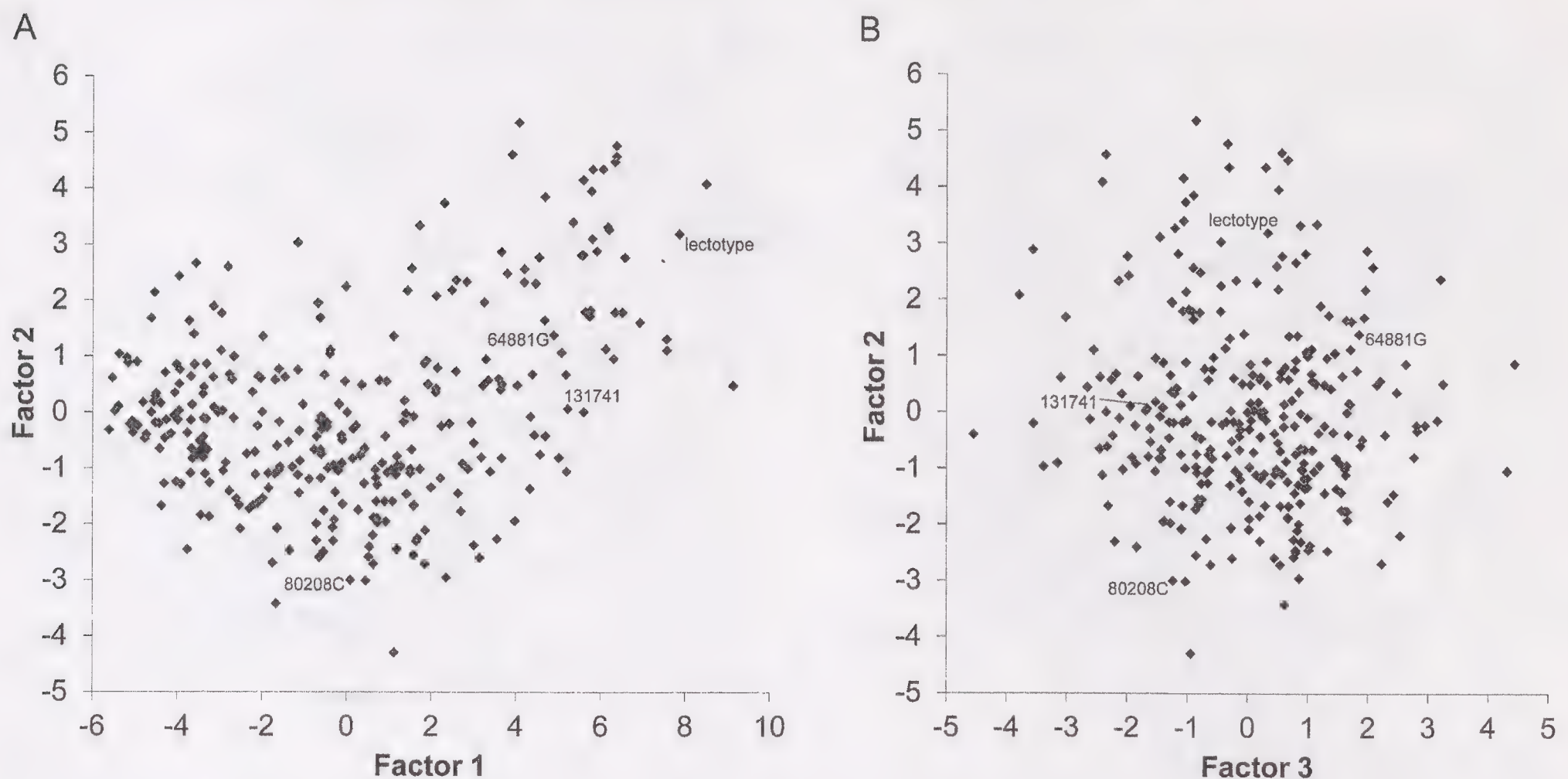


FIG. 6. Factor analysis plots showing individual specimens in factor space. FIG. 6A: Shells greater on factor 1 are larger (D, W, U, and have more beaded sculpture obsolescence [WBBW]). Shells greater on factor 2 begin rib obsolescence at smaller whorl number (WNOB), have fewer ribs per mm (RD), and have more beaded sculpture obsolescence (WBBW); FIG. 6B: Shells greater on factor 3 have a smaller initial whorl (W1) and a greater whorl expansion rate (WEXP). Shown are lectotype of *A. hybridum* (LT) and three specimens whose genitalia are illustrated in figure 8 (CM numbers indicated).

which obsolescence begins (WNOB) loaded strongly negatively on factor 2, with moderate negative loading of rib density (RD) and moderate positive loading of number of whorls back at which the beaded sculpture weakens (WBBW). Diameter of the first whorl (W1) loaded strongly negatively and whorl expansion rate (WEXP) loaded strongly positively on factor 3 (Table 1). The factor analysis plots show no hint of more than one group (Figs. 6A, 6B).

Shells scoring higher on factor 1 were larger, and their beaded surface sculpture had weakened on a greater amount of the last whorl, both features that are like *Ancotrema hybridum*, while those lower on factor 1 are more like *A. sportella*. Shells scoring higher on factor 2 had obsolescence of the surface sculpture beginning at a larger whorl number and fewer ribs per mm at whorl 4. We have no a priori information to predict which of those characters would correspond to which form, but this analysis suggests that the *A. hybridum*-like forms tended to initiate sculpture obsolescence later, and to have less dense ribs. Shells scoring higher on factor 3 had a larger diameter of whorl 1 and a smaller whorl expansion rate. As with factor 2, we have no a priori information to predict

which of these characters would correspond to which form.

Shells from the Puget Sound area seemed to be smaller than shells from other areas, so we explored shell size of specimens from different areas. On factor 1, the size factor, specimens from Puget Sound averaged smaller than those from southwestern Washington and southward (t-test of diameter, whorls, and umbilical diameter, all  $p < 0.001$ ) and 63% of Puget Sound specimens had smaller diameters than shells from any other geographical locality. *Ancotrema sportella*-like shells from the Puget Sound area and from southwestern Washington and southward were smaller (with very little overlap) than *A. hybridum*-like shells from southwestern Washington and southward (factor 1, Fig. 7A). However, *A. hybridum*-like shells from the Puget Sound area overlapped all three of those groups in size (factor 1, Fig. 7A). *Ancotrema sportella*-like shells from southwestern Washington and southward showed less variability in factor 1 (size) and factor 2 (diameter of whorl 1 and whorl expansion rate) than the other forms from other areas (Fig. 7A). None of the forms in either geographical area showed separation on factor 3 (Fig. 7B).



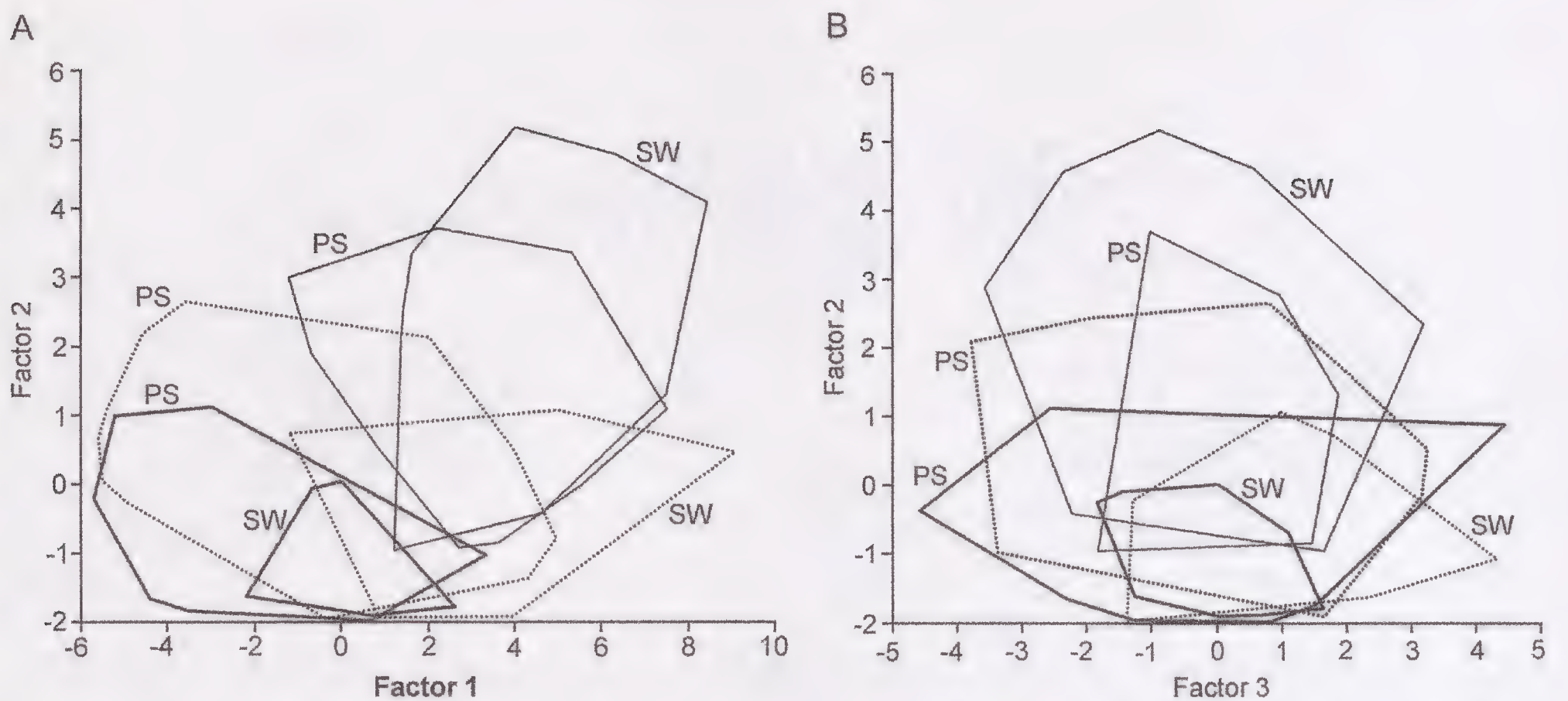


FIG. 7. Factor plots with minimum convex polygons surrounding *Ancotrema sportella* (heavy solid lines), *A. hybridum* (lighter solid lines), and unidentified shells (dotted lines). Separate polygons for each group show shells from the Puget Sound basin (PS) and from farther southwest (SW). FIG. 7A: Factors 1 and 2; FIG. 7B: Factors 2 and 3.

### Anatomy

The nine genital anatomies we examined were consistent with the anatomy illustrated by Pilsbry (1946) and did not show differences suggesting more than one species. In all anatomies, the base of the spermatheca duct is swollen, the length of the spermathecal duct was similar, and the ovate shape of the spermatheca was similar. The principal penial chamber contained six strong longitudinal pilasters below the sphincteric ridge.

The vagina is short and bore a muscular collar in most cases. The collar was not visible in one *A. hybridum* (CM80422) and its presence or absence was not discernable in the immature *A. sportella* (CM80145B). The size and shape of the collar varied among individuals irrespective of the form, but whether this variability was due to preservation is unknown. The collar of the figured *A. sportella* (Fig. 8A) is not large, but is evident on the left side of the vagina.

In both forms, the distal end of the vas deferens runs along the penis under a sheath and enters the penis at about its midpoint. In our anatomy illustrations (Fig. 8), the vas deferens of *A. hybridum* disappears under the sheath at the crotch between the penis and the vagina while in our *A. sportella* and in that of Pilsbry (1946: 228, fig. 112), the vas deferens did not disappear. However, the vas deferens disappeared at the crotch in three of five of the *A. hybridum* we dissected, and in two of four *A.*

*sportella* (including Pilsbry's illustration). That feature appears to be an artifact of the dissection and not a consistent difference between forms.

We did note some differences in the path the vas deferens took in traveling along the free oviduct. In some individuals, it was close to the free oviduct and in others it was far from that structure (possibly an artifact of contraction upon preservation or of the dissection itself), and in some individuals the vas deferens made a loop (or in one case, two loops). None of these features seemed to separate the two forms. In three of four *A. hybridum* and two of three *A. sportella*, the vas deferens was adnate to the free oviduct. In three of four *A. hybridum* the vas deferens had a loop and in the one of three *A. sportella* having a looped vas deferens there were actually two loops. The loop coiled clockwise in one of the three *A. hybridum* having a looped vas deferens and in the *A. sportella* with a looped vas deferens, both loops were clockwise.

The three *A. hybridum* and one *A. sportella* whose apical penial chambers we examined and the illustration of *A. sportella* by Pilsbry (1946: 228, fig. 112) showed plications above a sphincteric ridge, but there was variability in the arrangement of these structures. We do not know whether the variability could be taxonomically significant, or whether differences could be individual variation or even the result of the dissections. In short, we saw no anatomical



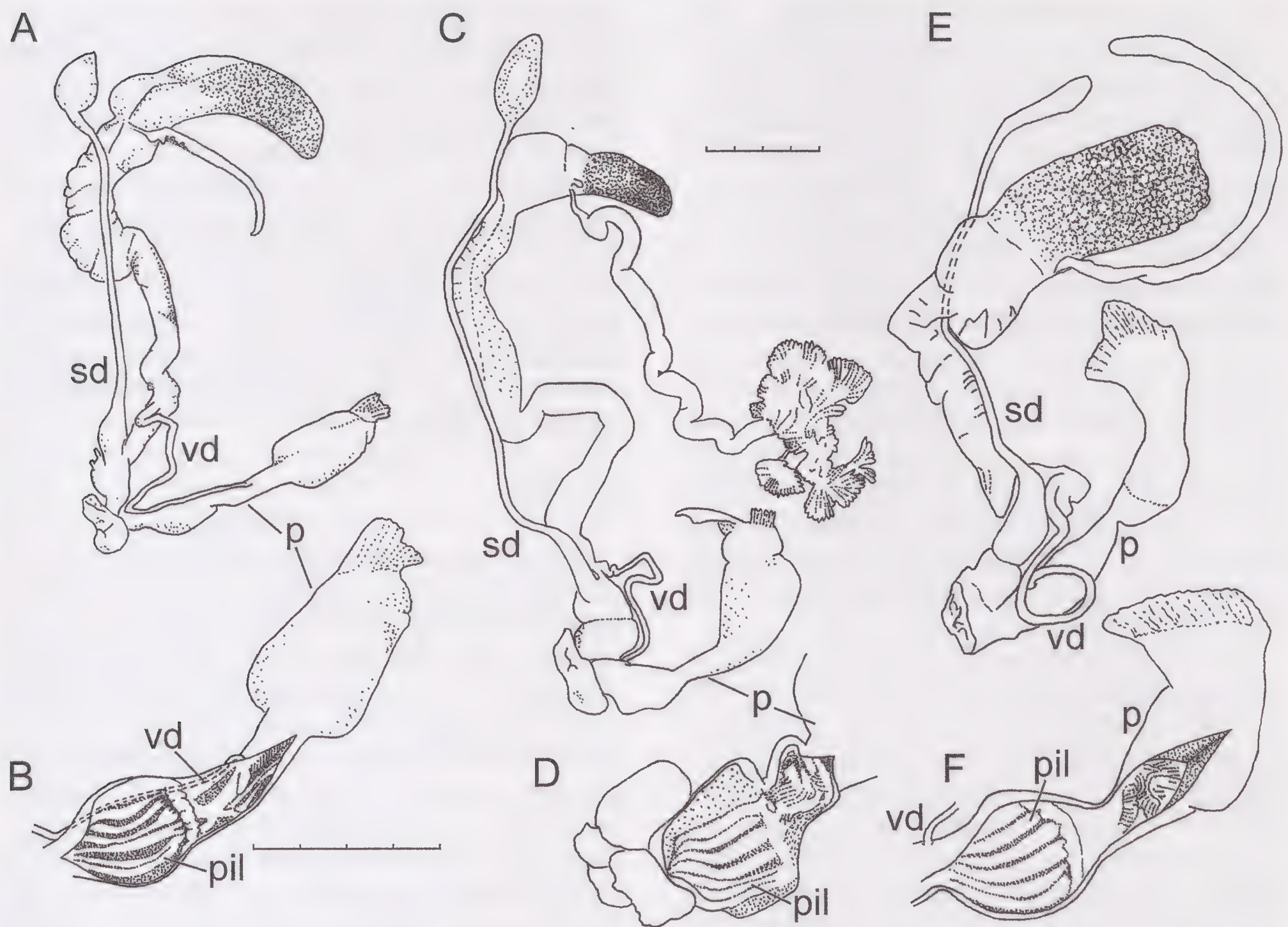


FIG. 8. Genital anatomies of *Ancotrema*. FIG. 8A, B: *Ancotrema sportella* CM80208C from Lane Co., Oregon; FIG. 8C, D: *Ancotrema hybridum* CM132741 from Multnomah Co., Oregon; FIG. 8E, F: *Ancotrema hybridum* CM64881G from Lewis Co., Washington. A, C, E (upper scale bar): genitalia overview; B, D, F (lower scale bar): split penis detail. Scale bars = 4 mm. Abbreviations: p – penis; pil – pilaster; sd – spermathecal duct; vd – vas deferens.

differences that would suggest the specimens are more than one species.

The base of the spermathecal duct in *Haplotrema* s.s. is little or not swollen and they have a longer vagina (according to illustrations in Pilsbry, 1946), suggesting that the swollen base and short vaginas in *Ancotrema* might be synapomorphies for this group.

## DISCUSSION

### Shell Morphometry

We found no evidence of bimodality in any shell character, particularly in the character previously used to support separate species (obsolescence of ribs on last whorl). This lack of bimodality fails to support the existence of two species, and hence suggests the two forms are one species.

Although Baker (1931) conceived *A. sportella* to be a smaller form (< 18 mm diameter) occurring in the Puget Sound area and *A. hybridum* to be a larger (> 18 mm) more widespread form, we found large and small individuals having sculpture features of both forms in the Puget Sound area (Fig. 7A, factor 1 represents size variables). This finding falsifies the use of size to separate the forms.

The two forms, *Ancotrema sportella* and *A. hybridum*, are traditionally separated by obsolescence of radial ribs on the last one or two whorls. This point of reference counts number of whorls backward from the end of growth rather than forward from the beginning of growth. It is a convenient, easily recognized feature. However, this traditional method of separating the forms does not address identification of specimens whose diminished sculpture extends between zero and one whorl back.



We found that the number of whorls back having weak sculpture varied continuously from zero to 1.5 whorls. Furthermore, we found for both forms, that the radial sculpture weakened at about five whorls, regardless of the total number of whorls in the adult shell (Fig. 5). Applying the traditional identification method, a snail that stopped growing about whorl five would be classified as *A. sportella*, while one that grew to whorl six would have an entire whorl with weakened sculpture and would be classified as *A. hybridum*. Notable is the fact that the lectotype of *A. hybridum* is one of the most extreme *Ancotrema* specimens in size (Fig. 6A). The fact that sculpture diminished near whorl number five, and that the distance back at which it diminished was continuously variable, fails to support the existence of two different species.

Obsolescence of ribs began at approximately the same point in all specimens, indicating that the start of obsolescence seems to depend on developmental whorl number rather than ultimate shell size. The point at which obsolescence begins increased slightly with whorl number, but this increase does not change the fact that the onset of obsolescence seems to be a function of whorl number rather than a species difference.

We propose a new hypothesis: in contrast to two separate species, those forms called *Ancotrema sportella* are the individuals that stopped growing about the same time their ribs weakened, about whorl five, while those called *A. hybridum* are those that continued growing after their ribs weakened, about whorl five.

### Exploring Morphology by Geography

The ranges of the two forms overlap from northern California to the Aleutian Islands, Alaska (Roth & Sadeghian, 2003).

Shells from the Puget Sound region showed a greater size range than *Ancotrema* from southwestern Washington and southward. Adult specimens from Puget Sound included shells that were much smaller than those from farther south (Fig. 7A). Two hypotheses that might explain greater size variability in the Puget Sound region are: (1) snails that moved from farther south after glaciers retreated might have experienced relaxed selection (Lahti et al., 2009) or (2) snails from refugia during the last glacial maximum (Schafer et al., 2010) would have been isolated from snails farther south and

therefore might have experienced drift or selection. These hypotheses are plausible, given that other biota have been shown to differ between the Puget Sound region and surrounding areas (Wei et al., 2011; Larson et al., 2012).

A molecular clock could differentiate between these hypotheses. With colonization from the south, Puget Sound and southern populations would show divergence after the glacial retreat about 12,000 years ago, while populations in refugia would have separated from southern populations after the glacial maximum about 18,000 years ago.

### Anatomy

We found no meaningful differences in the genital anatomies between the two forms. Spermathecal ducts of both forms are swollen at their bases. Penes in both forms have six pilasters. The vas deferens in both forms is adnate along the base of the penis to its point of insertion. This result corroborates previous literature reports and further weakens the possibility that these two forms are separate species. Baker (1931) reported that the anatomy of *Ancotrema hybridum* from Riverdale and Astoria were “essentially the same as that of typical *sportella*.” Roth’s (1991) comparison of his own dissection from Cape Blanco, Curry Co., Oregon, and that of Webb (1961) did not show any unequivocal differences in genitalia between the two forms.

The muscular collar on the vagina is a feature that is basal within Haplotrematinae and is a feature of the genus *Ancotrema* (Roth, 1991). Although the collar on the illustrated *A. sportella* is less obvious than those of the illustrated *A. hybridum* (Fig. 8), size and shape of the collar varied among individuals irrespective of their shell form.

### Ecological Considerations

If *Ancotrema hybridum* really is just an overgrown *A. sportella*, and if environmental conditions influence whether an individual stops at *A. sportella* morphology or continues growing into *A. hybridum* morphology, and since individuals can live multiple years, then the two forms theoretically could be found in the same place, as reported by Roth (1990, 1991). In *Ancotrema*, one individual could grow under poor conditions one year to become a small adult while a neighbor individual could



grow to be a larger adult with *A. hybridum* morphology under more favorable conditions in the following year. Under this scenario, two individuals of the same species could have different morphologies and be found in the same place together.

The sculpture diminishment seems decoupled from other ontogenetic changes related to fully grown shells, generally considered (but not demonstrated for most species) to coincide with sexual maturity. Such ontogenetic changes in *Ancotrema* include suture descending, upper lip turning downward, and lip edge thickening and reflecting slightly especially on the lower edge. Furthermore, the sculpture diminishment seems decoupled from environmentally induced changes such as resting marks on the shell. Instead, the sculpture diminishment occurs near whorl number five. The significance of this change at whorl five is not clear, but that whorl number might be influenced by allometry or by the tradeoff of growing larger (to make more eggs in the future) versus reproduction before dying.

A future experiment could raise juveniles from a single batch of eggs to examine whether the snails will grow to different morphologies under different environmental conditions. Environmental conditions that might influence final size include moisture availability (Goodfriend, 1986), food availability and possibly food type. These species are omnivorous; it would be interesting to see whether the proportion of animal to plant food would influence the adult morphology.

Other species are currently included in *Ancotrema*, but we did not examine them for this analysis. Anatomical differences pointed out by Pilsbry (1946), such as the longer vagina of *A. voyanum* (Newcomb, 1865), suggest it is likely to be a distinct species. Although soft part anatomy was not available for the description of *A. zopherum* Roth, 1990, distinct shell features suggest it to be a distinct species. Future examination of *A. sportella sinkyonum* Roth, 1990, could examine whether it should continue to be considered a separate subspecies of *A. sportella*.

This examination of shell characteristics and internal anatomy shows no morphological evidence that *Ancotrema hybridum* and *A. sportella* are separate species. None of the morphological characteristics that we examined showed bimodality. Thus, we conclude that *A. hybridum* should be considered a junior synonym of *A. sportella*.

## ACKNOWLEDGMENTS

We are grateful to Amanda Zimmerman for producing the shell measurement figure and helping with the anatomy figure. Timothy Dolan produced the distribution map. Barry Roth provided helpful comments on an early draft and pointed out the ambiguity of which form should bear the name *A. sportella*. Three anonymous reviewers helped to improve the manuscript.

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## STRESS RESPONSE AT THE CELLULAR AND BIOCHEMICAL LEVELS INDICATES THE LIMITATION OF THE ENVIRONMENTAL TEMPERATURE RANGE FOR EASTERN SIBERIAN POPULATIONS OF THE COMMON GASTROPOD *LYMNAEA STAGNALIS*

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### ABSTRACT

Temperature is a major environmental factor that influences all aquatic organisms. Our objective was to expose individuals of *Lymnaea stagnalis* from an Eastern Siberian population to wide temperature gradients to determine whether they express a thermal stress response and what mechanisms are involved in this process. Several parameters of the cellular mechanisms of thermal resistance were tested under the experimental conditions: the level of lipid peroxidation, the synthesis of heat shock protein HSP70, the activities of antioxidative enzymes and changes in the content of energy-associated metabolites.

The results of this study show that the temperature at which the cellular and biochemical stress-response is activated in the *L. stagnalis* from Eastern Siberian lakes directly corresponds to environmental temperature within the range of 3 to 15°C. The exposure of the gastropods to temperatures outside this range resulted in the activation of HSP70 synthesis, changes in the activities of antioxidative enzymes and glycogenic metabolism. These conditions can be considered to be stressful to the tested gastropods. Because *L. stagnalis* is a common species that inhabits a wide range of lakes with temperatures higher than 15°C, we suggest that the limitation established by this study can be considered to be the result of a local temperature adaption of the Eastern Siberian population. This diversity of temperature adaptation among different populations of *L. stagnalis* contributes to the common environmental variation and plasticity of the species, which is strongly reflected at the levels of cellular and biochemical processes and the gastropods' stress reactions.

Key words: gastropods, *L. stagnalis*, stress, stress-response, thermal gradient.

### INTRODUCTION

Temperature is a major environmental factor that influences all aquatic organisms. With respect to temperature preferences, all aquatic organisms can be divided into two groups: the eurythermic species, which inhabit a wide temperature range; and the stenothermic species, which prefer a narrow temperature range. Thus, the growth, development and metabolism of the organisms depend strongly on the environmental temperature (Pörtner & Knust, 2007). Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia. The atmosphere

and ocean have warmed, the amounts of snow and ice have diminished, sea level has risen and the concentrations of greenhouse gases have increased (Stocker et al., 2013). Currently, repercussions of thermal pollution and global warming are increasing in the Holarctic ecosystems. The increase of the average temperature in water reservoirs has a negative effect on their biota. In this context, studies of the theoretical and predictive values for assessing the impact of thermal pollution and global warming on the freshwater biota have a great significance (Pörtner & Giomi, 2013).

Pulmonate gastropods, for which the species distribution, biodiversity and abundance vary in different freshwater bodies, are promising

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model organisms for temperature adaptation studies. Mollusks are a permanent component of the trophic chains in ecosystems, and *Lymnaea stagnalis* is known to be one of the most common pulmonate gastropod species in freshwater bodies, as previously stated by Linnaeus (1758), Rivaz et al. (2014) and others. This species is widely distributed in the Holarctic zone (Skorping, 1985). Due to a wide distribution of this species, *L. stagnalis* is characterized by high conchological variety, metabolic plasticity and the ability to vary thermal resistance mechanisms of adaptation to environmental temperature changes (Ducrot et al., 2010; Coutellec et al., 2013; Haarder et al., 2013).

The common Palearctic gastropod species *Lymnaea stagnalis* was chosen as the subject for this study. This species is omnivorous and typically inhabits a littoral zone of numerous freshwater ponds from 0 to 3 meters (Timoshkin, 2001; Sitnikova & Starogogatov, 2004; Besnard et al., 2013). This species inhabits many Eastern Siberian lakes, including the shallow water basins and bays of Lake Baikal (Kozhov, 1936; Timoshkin, 2001). Individuals of *L. stagnalis* exist in different temperature ranges of water bodies, from 1–2°C to 30–32°C (Golubev et al., 2011, 2013). Temperatures of 30–32°C are close to the upper tolerance threshold of most aquatic organisms. *Lymnaea stagnalis* easily adapts to laboratory conditions and lives in these conditions without loss of activity or nutrition. The wide distribution of this molluscan species in the Holarctic region and the quality of its stress-resistance mechanisms makes it a promising model species for laboratory and environmental studies.

We make the assumption that *L. stagnalis* represents an Eastern Siberian population has a limiting degree of thermal resistance mechanisms due to a local adaptation to the predominantly low temperature regime of the aquatic environments there.

## MATERIALS AND METHODS

### Animals

Animals were collected on aquatic plants in several typical freshwater lakes located near the city of Irkutsk (Irkutsk region, Eastern Siberia, Russia). The GPS coordinates of sampling is following: 52.268001, 104.280998; 52.268086, 104.284055. No specific permissions were required for this sampling. The animals' shell

heights were 3.1–3.7 cm ( $n = 45$ ), whereas their weights (with shell) were 5.1–8.5 g ( $n = 45$ ). The gastropods were pre-acclimated for one week in filtered natural water at constant conditions of 6°C (the average temperature in the selected environment) and intense aeration. During the acclimation period, the gastropods were fed *ad libitum* with Tetramin food (Tetra, Germany).

### Experimental Design

To examine the animal's thermal tolerance at the biochemical level, two types of experiments were performed. In the first, the gastropods were exposed to a gradual temperature increase of 1°C per hour, beginning at the temperature of pre-acclimation (6°C) and increasing to 30°C (a maximal established summer temperature of the lake of the gastropods' origin). The second involved exposure of the gastropods to a gradual temperature decrease at a constant rate beginning at the temperature of the pre-acclimation (6°C) and decreasing to 0.5°C (a minimal temperature for the animal's activities before the freezing point of water). The rate of temperature decrease was 1°C per hour, the same as in case of gradual hyperthermia experiments (modified method described by Sokolova & Pörtner, 2003).

Control samples were collected from an aquarium with a temperature of 6°C before the experiments. After every 5 degrees of temperature increase (10°C, 15°C, 20°C, 25°C, 30°C) and after every 3 degrees of temperature decrease (3°C, 0.5°C), 2–3 specimens (whole organisms) were collected from each of five aquaria and flash-frozen in liquid nitrogen. Thus, up to 100 animals were used for current research.

### Biochemical Methods

Several parameters of the cellular mechanisms of thermal resistance were tested under the experimental conditions. These included the level of lipid peroxidation, synthesis of the heat shock protein HSP70, activities of anti-oxidative enzymes, and changes in content of energetic metabolites.

**Lipid Peroxidation Level:** To determine the lipid peroxidation level, the concentration of Schiff's bases was measured (Pietrzak et al., 2010; Axenov-Gribanov et al., 2014). Spectrophotometric analysis of the samples was performed at  $\lambda = 400$  nm in quartz cuvettes.



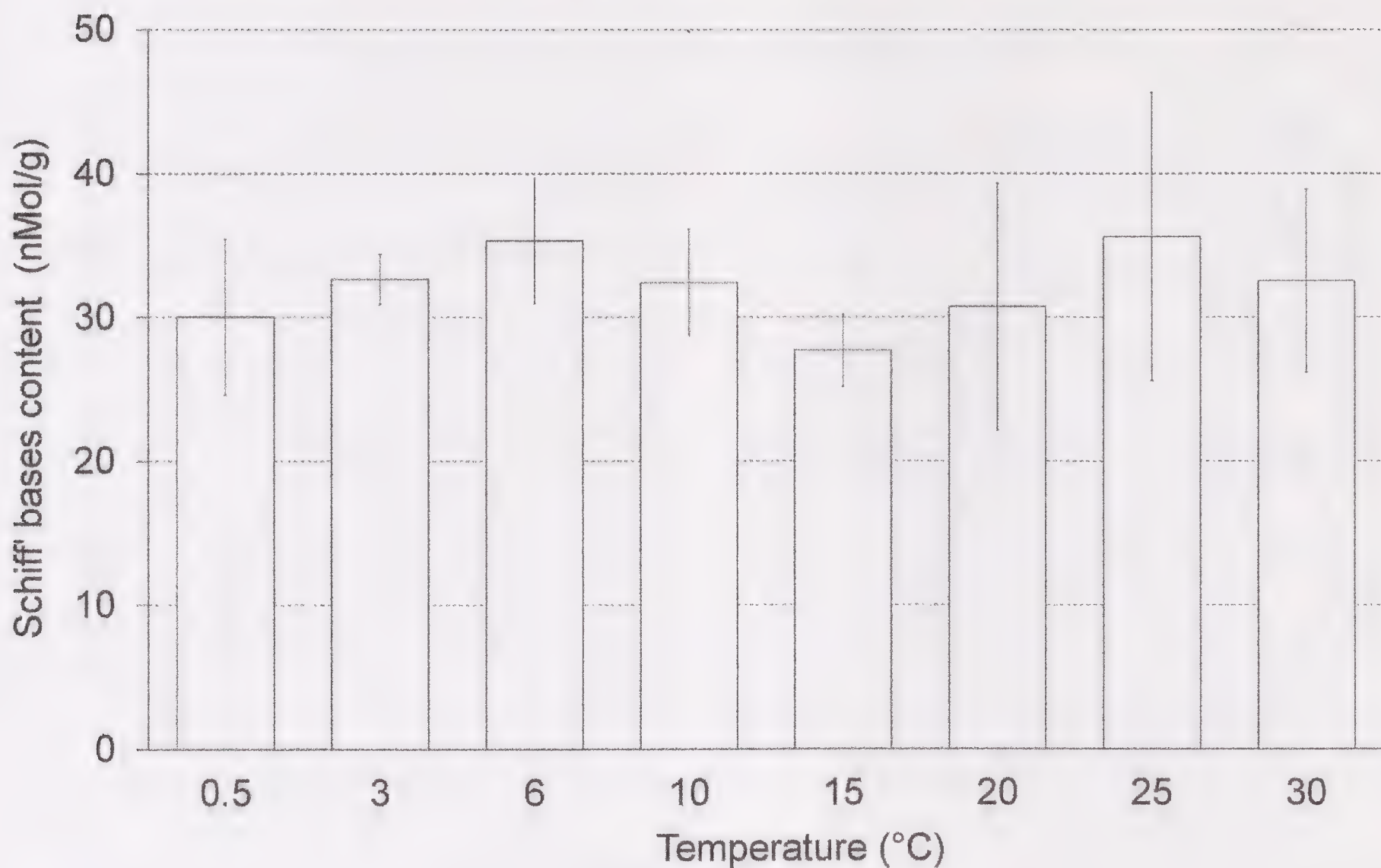


FIG. 1. Schiff's bases levels in gastropod species *L. stagnalis* exposed to gradual thermal challenge from 6°C (control) to 0.5°C and 6°C (control) to 30°C. \*Indicates significant difference ( $P < 0.05$ ) from the control (6°C).

**HSP70 Level:** The concentration of HSP70 was determined using SDS-PAGE electrophoresis followed by Western blotting (Bedulina et al., 2013). The antibodies used for the HSP70 Western blotting were as follows: first antibody - monoclonal anti-heat shock protein 70, produced in mouse – № H5147 (Sigma Chemical Co); secondary polyclonal anti-mouse antibody – Stressgen, № SAB-101. As an internal reference control, actin levels were also estimated. The antibodies used for the Western blotting for actin were as follows: first antibody, polyclonal anti-Actin antibody produced in rabbit № A2668, (Sigma Chemical Co); secondary anti-rabbit antibody № A9919 (Sigma Chemical Co). The blotted PVDF membranes were washed several times in TTBS solution between the incubations with each antibody solution. The protein-antibody complexes were detected using BCIP-nBT. Densitometric analysis was performed using ImageJ Software v.1.41 (Wayne Rasband).

**Antioxidative Enzymes Activity:** Activities of the antioxidative enzymes (peroxidase, catalase, and glutathione S-transferase) were estimated using the methods by Drotar et al. (1985), Habig et al. (1974) and Aebi (1984)

(modified according to Timofeyev et al., 2008; Bedulina et al., 2010), using wavelengths of  $\lambda = 340$  nm for peroxidase and  $\lambda = 240$  nm for catalase. The activity of lactate dehydrogenase was determined by the express-kit "LDH-vital" (Vital-Diagnostics Spb, Russia) at  $\lambda = 340$  nm.

**Energetic Metabolites:** Levels of glucose, glycogen, L-arginine, and phospho-L-arginine (PLA) were measured using NADH/NADPH-dependent enzymatic methods at  $\lambda = 340$  nm which previously stated (Bergmeyer & Bergmeyer, 1985; Grieshaber et al., 1994; Sokolova et al., 2012). Deposited energetic metabolites (glycogen and PLA) were hydrolyzed using the methods described by Ivanina et al. (2010) and Morris et al. (2005). Levels of lactate were determined using the express-kit "Lactate-vital" (Vital-Diagnostics Spb, Russia) at  $\lambda = 505$  nm. All spectrophotometric measurements were performed with a Cary 50-spectrophotometer (Varian, USA).

#### Statistics

All experiments were performed with 5 biological replicates, and biochemical measurements were performed in triplicate for each sample.



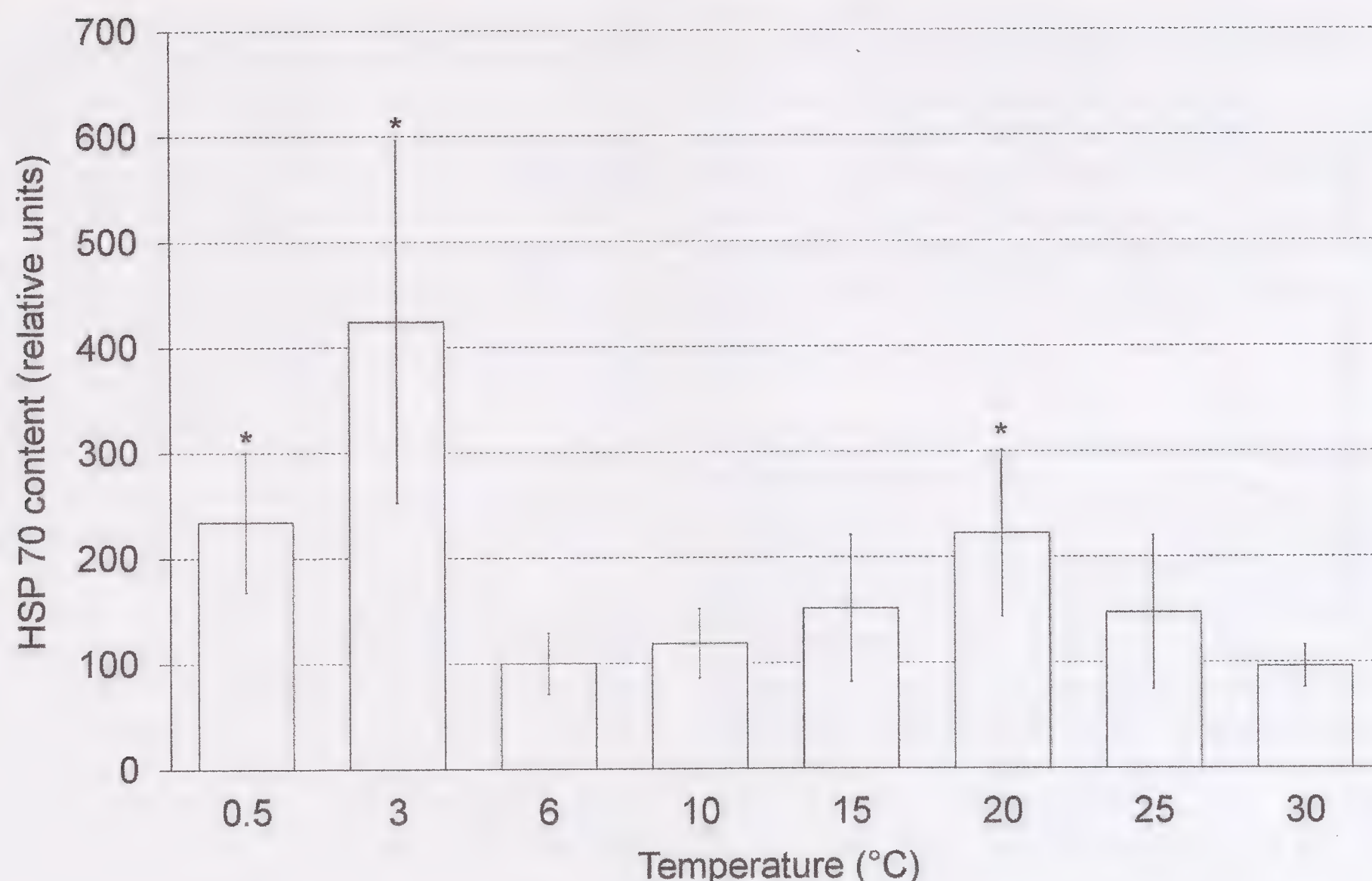


FIG. 2. HSP70 levels in gastropod species *L. stagnalis* exposed to gradual thermal challenge from 6°C (control) to 0.5°C and 6°C (control) to 30°C. \*Indicates significant difference ( $P < 0.05$ ) from the control (6°C).

Data were analyzed statistically using one-way Analysis of Variance (ANOVA, general linear model) and the statistical package, Statistica 8.0 (StatSoft). Correlation analysis was used to quantify the relationship of measured parameters to temperature and between each other. Differences were considered to be significant at  $P < 0.05$  (alpha 0.05). The results were compared with those from control groups.

## RESULTS

The concentration of the Schiff's bases in the control group of *L. stagnalis* were 30.93–39.67 nMol/g wet weight. The temperature exposure gradients between 0.5–30°C did not change Schiff's base content in *L. stagnalis* (Fig. 1).

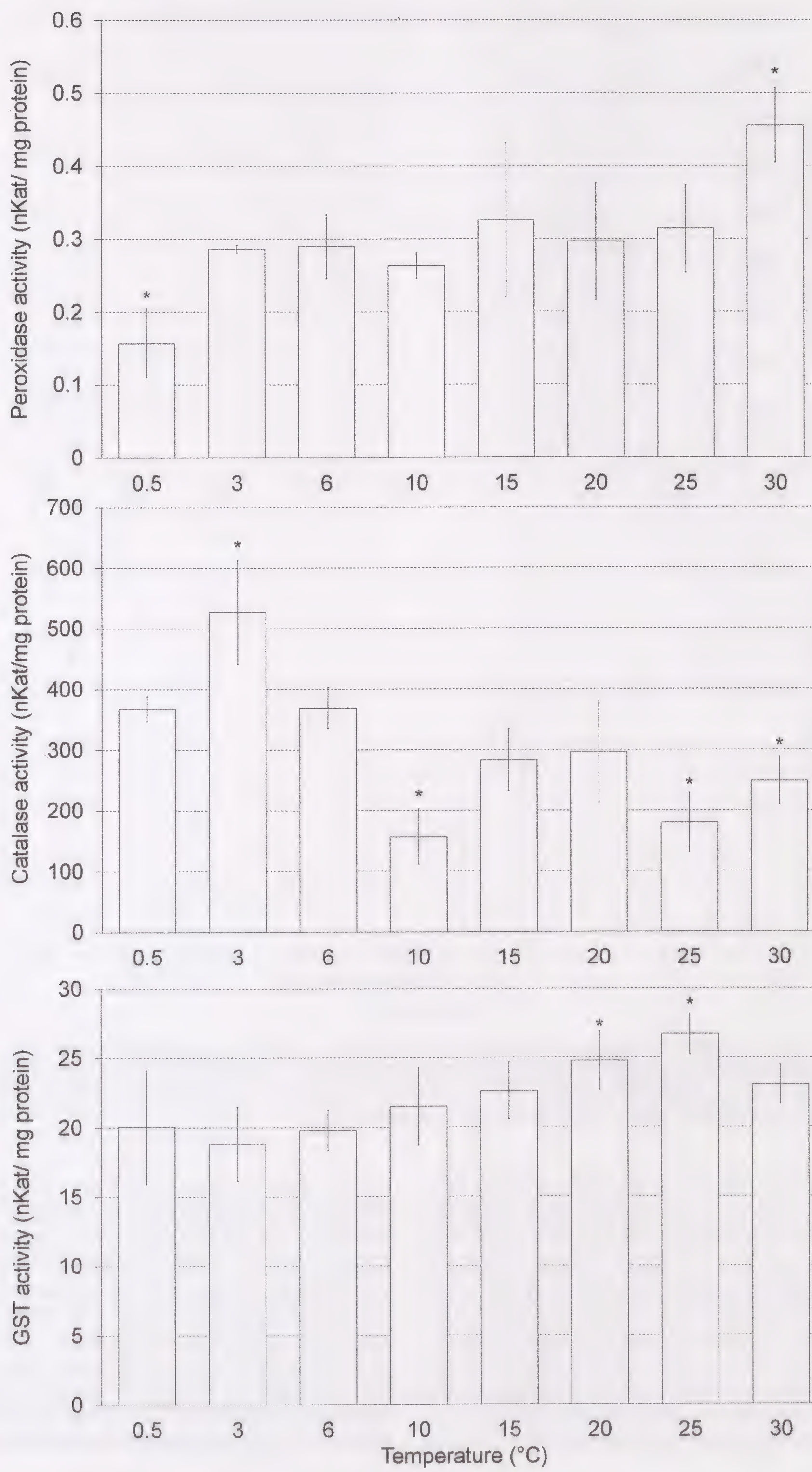
HSP70 with a molecular mass of approximately 70 kDa was detected in the control animals. The amount of HSP70 increased significantly to 122% of the control level at 20°C during the temperature increase experiment

and to 324% at 3°C in case of the temperature decrease experiment (Fig. 2). The level of HSP70 accumulation at 3°C was much higher than that observed at 20°C.

The basal levels of the peroxidase, catalase and glutathione S-transferase activities were  $0.29 \pm 0.04$  nKat/mg protein,  $19.78 \pm 1.47$  nKat/mg protein and  $369.32 \pm 33.86$  nKat/mg protein, respectively. The values for the activities of the antioxidative enzymes were constant in the temperature range 3–25°C for peroxidase and 0.5–15°C for glutathione S-transferase. The gradual temperature increase to 30°C and 20°C resulted in increases in the peroxidase ( $0.45 \pm 0.05$  nKat/mg protein) and glutathione S-transferase activities ( $23.07 \pm 1.39$  nKat/mg protein) respectively. The gradual temperature decrease to 0.5°C resulted in a decrease in peroxidase activity ( $0.15 \pm 0.04$  nKat/mg protein). Catalase activity also changed during the temperature gradient exposure. The increase in the temperature to 10°C resulted in a significant decrease in catalase activity

FIG. 3. Peroxidase, catalase and glutathione S-transferase activities in gastropod species *L. stagnalis* exposed to gradual thermal challenge from 6°C (control) to 0.5°C and 6°C (control) to 30°C. \*Indicates significant difference ( $P < 0.05$ ) from the control (6°C).







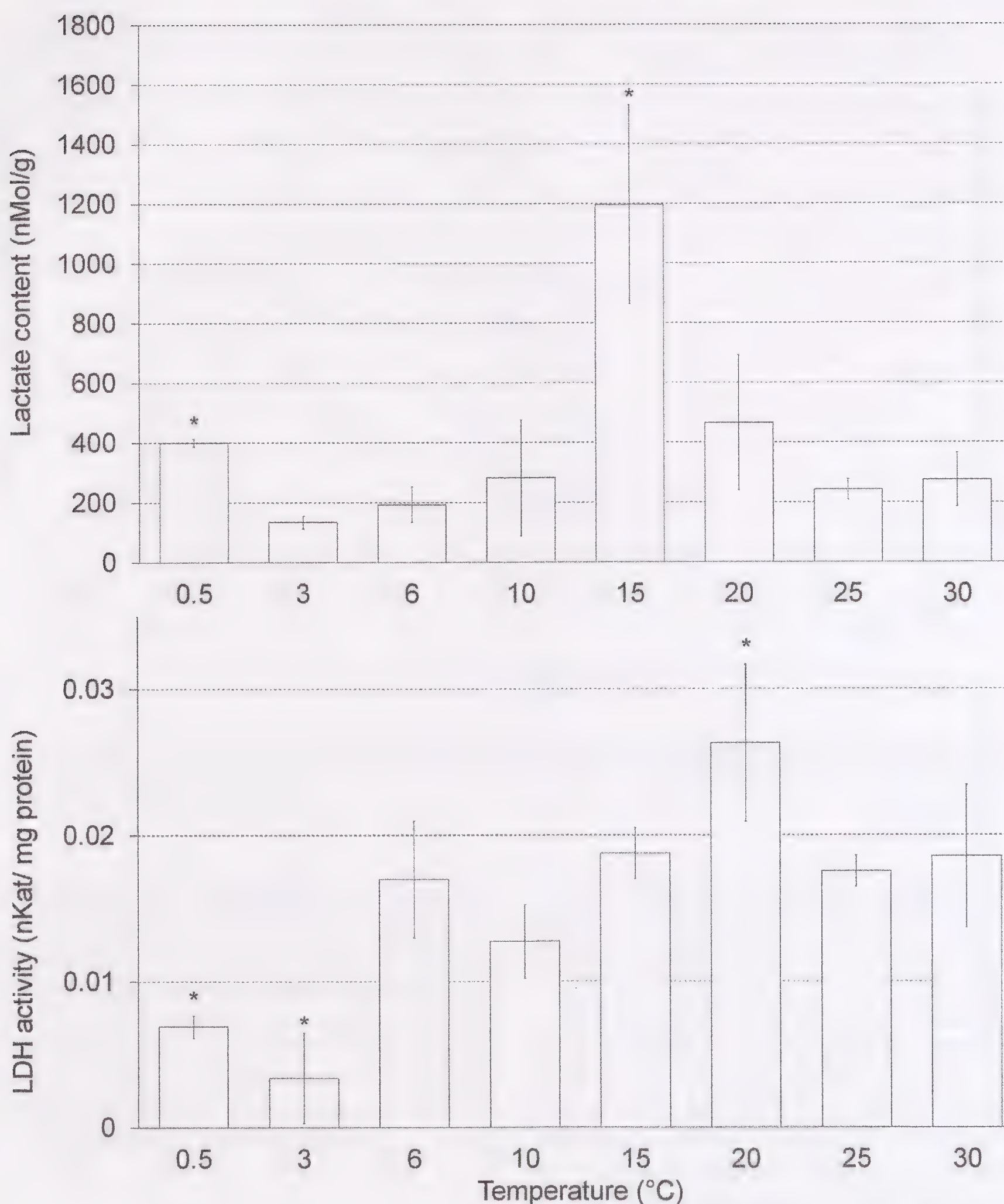


FIG. 4. Lactate content and lactate dehydrogenase activities in gastropod species *L. stagnalis* exposed to gradual thermal challenge from 6°C (control) to 0.5°C and 6°C (control) to 30°C. \*Indicates significant difference ( $P < 0.05$ ) from the control (6°C). \*Indicates significant difference ( $P < 0.05$ ) from the control (6°C).

( $156.9 \pm 45.3$  nKat/ mg protein), and the decrease to 3°C resulted in a significant increase in the catalase activity ( $527.4 \pm 85.9$  nKat/ mg protein) (Fig. 3).

The basal concentration of lactate and the lactate dehydrogenase activity in the control group of *L. stagnalis* were  $192.53 \pm 59.35$  nMol/g wet weight and  $0.017 \pm 0.004$  nKat/ mg protein respectively. These values were stable in the temperature range 3–10°C for lactate content and in the range 6–15°C for

lactate dehydrogenase activity. The gradual temperature increase to 15°C and the decrease to 0.5°C resulted in changes in the lactate concentration to  $1196.92 \pm 333.97$  nMol/g wet weight and  $134.09 \pm 22.16$  nMol/g wet weight, respectively. The maximal concentration of lactate at 15°C was much greater than that at 0.5°C. The lactate dehydrogenase activity rose to  $0.026 \pm 0.005$  nKat/mg protein at 20°C during the temperature increase exposure. In contrast, the lactate dehydrogenase activity fell



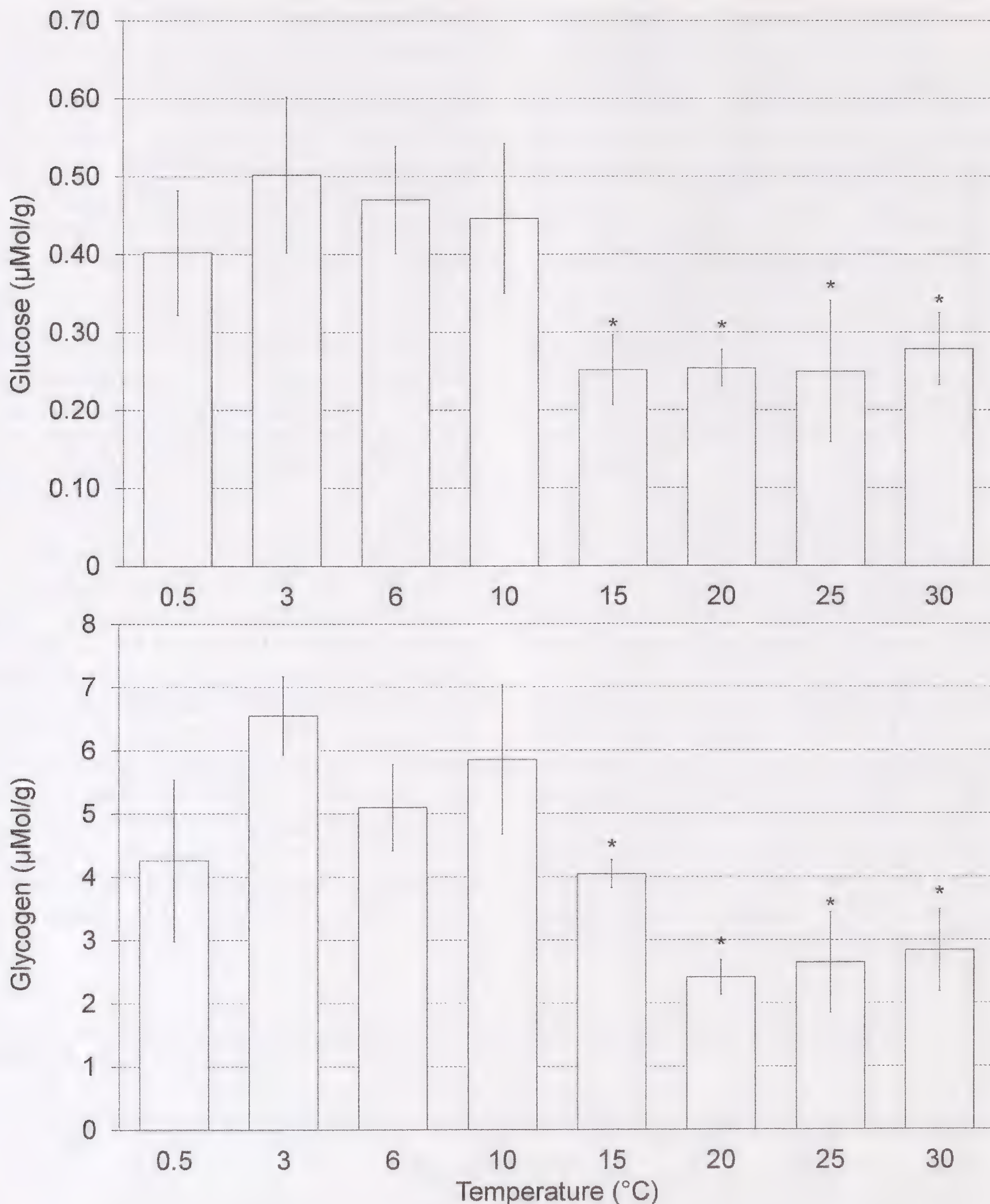


FIG. 5. Glucose and glycogen levels in gastropod species *L. stagnalis* exposed to gradual thermal challenge from 6°C (control) to 0.5°C and 6°C (control) to 30°C. \*Indicates significant difference ( $P < 0.05$ ) from the control (6°C). \*Indicates significant difference ( $P < 0.05$ ) from the control (6°C).

to  $0.006 \pm 0.0007$  nKat/mg protein at temperatures between 3 and 0.5°C during temperature decrease exposure (Fig. 4).

The concentration of glucose associated with glycogen in the control group of *L. stagnalis* was  $5.10 \pm 0.68$  μMol/g wet weight, and the concentration of free glucose was  $0.47 \pm 0.07$  μMol/g wet weight. The exposure to the gradual temperature increase led to significant decreases in both glycogen and free

glucose. The concentrations of free glucose and glycogen began to decrease at 15°C and the decreases continued until the end of the exposure. The minimum glucose concentration was observed at 25°C ( $0.25 \pm 0.09$  μMol/g wet weight), and the minimum glycogen concentration was observed at 20°C ( $2.41 \pm 0.27$  μMol/g wet weight) (Fig. 5). The maximum concentrations of glucose and glycogen were observed at 3°C, and the most attenuated levels of



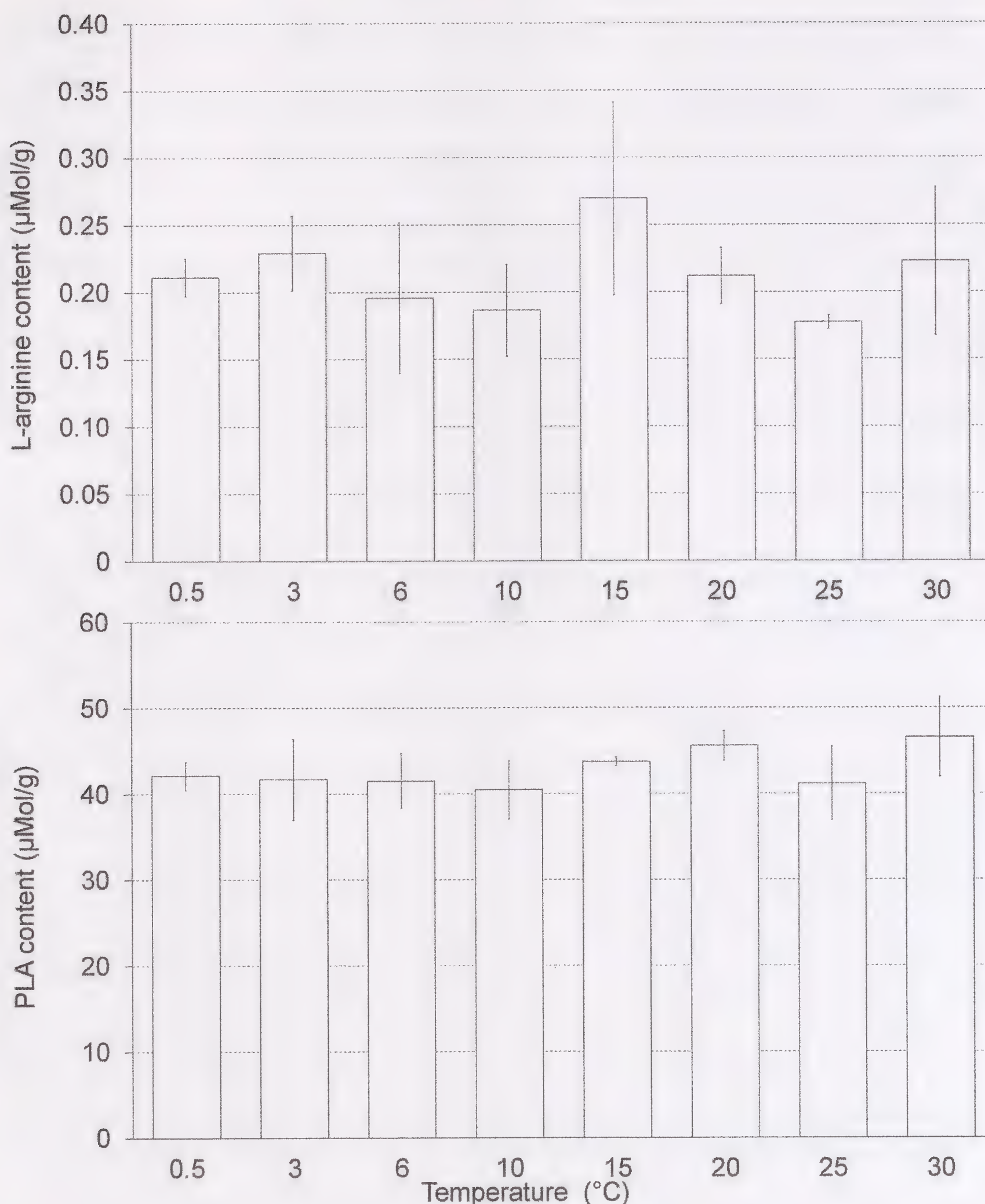


FIG. 6. L-arginine and phospho-L-arginine levels in gastropod species *L. stagnalis* exposed to gradual thermal challenge from 6°C (control) to 0.5°C and 6°C (control) to 30°C. \*Indicates significant difference ( $P < 0.05$ ) from the control (6°C). \*Indicates significant difference ( $P < 0.05$ ) from the control (6°C).

glucose and glycogen were observed between 15 and 20°C.

The concentration of deposited phospho-L-arginine in the control group of *L. stagnalis* was  $40.48 \pm 3.42$  μMol/g wet weight, and the concentration of L-arginine in these animals was  $0.19 \pm 0.05$  μMol/g wet weight. The concentrations of L-arginine and PLA did not change during the exposures over the temperature range of 0.5–30°C (Fig. 6). The greatest attenuation of L-arginine and PLA were observed at 10°C.

## DISCUSSION

These results indicate that a gradual temperature change leads to the activation of a number of thermal resistance mechanisms and alterations in the energetics of the glycogenic processes in specimens of *L. stagnalis* representing an Eastern Siberian population.

The current study results indicate that each of the tested metabolic parameters was stable within a specific temperature range. The stable



ranges were 3–10°C (for lactate content), 0.5–10°C (for glucose and glycogen content), 6–15°C (for HSP70 and lactate dehydrogenase activity), 0.5–15°C (for glutathione S-transferase), 3–25°C (for peroxidase activity), and 0.5–30°C (for Schiff’s bases, L-arginine and PLA). Exposure of the gastropods to conditions beyond these temperature ranges provoked the activation of cellular and biochemical stress-response mechanisms. Both gradual hypothermia and hyperthermia led to increases in HSP70 and lactate. The temperature increase led to the depletion of energetic metabolites such as glucose and glycogen due to a switch from aerobic to anaerobic metabolism. A significant activation of the antioxidative enzymes (peroxidase and glutathione S-transferase) and lactate dehydrogenase was also observed in *L. stagnalis* during the exposure to gradually increasing temperatures. The activity of catalase decreased during the increase in temperature, but it increased during the temperature decrease. In contrast, the activity of lactate dehydrogenase increased during the increases in temperature and decreased during the temperature decreases. It is assumed that the studied biochemical parameters are markers of metabolic processes. Thus, we consider that the possible causes and functional consequences of the changes we obtained are indicators of a stressed condition of the animals.

As mentioned above, HSP70 is one of the most significant markers of a stress response. The HSPs are molecular chaperones, and their main role is to restore a native conformation and functional activity of damaged proteins as previously stated (Shatilina et al., 2011; Bedulina et al., 2013). The accumulation of HSP70 in relation to decrease in temperature was greater than that observed during the increase in temperature. This indicates that the tested specimens of *L. stagnalis* can be considered to be thermally sensitive. Thus, the accumulation of HSP70 in *L. stagnalis* protects the cell proteins from non-optimal temperatures, thereby maintaining protein homeostasis (Afonso et al., 2008).

The energy deficit observed in *L. stagnalis* under exposure to non-optimal temperatures is due to the disruption and/or deregulation of the mitochondrial electron transport chain. This leads to a switch from aerobic to anaerobic metabolism (Sokolova & Pörtner, 2003; Philp et al., 2005). The activation of anaerobiosis was observed in this study as the accumulation of lactate and changes in lactate dehydrogenase activity. These are major regulators of redox processes, NAD/NADH balance and glycolytic circles (Mathews et al., 2000). The contents of glucose and glycogen, which are involved in the glycolytic cycles, decreased during the temperature increases. Thus lactate is one of the main energy-associated metabolites in this

TABLE 1. Correlation analyses of some cellular and metabolic assessment parameters in the Palearctic gastropod *Lymnaea stagnalis* from Baikal region.

|                              | Tem-<br>perature | HSP70 | LDH   | Lac-<br>tate | Peroxi-<br>dase | Cata-<br>lase | Glutathi-<br>one S-<br>transferase | L-Argi-<br>nine | PLA   | Glu-<br>cose | Glyco-<br>gen |
|------------------------------|------------------|-------|-------|--------------|-----------------|---------------|------------------------------------|-----------------|-------|--------------|---------------|
| Temperature                  |                  | -0.49 | 0.71  | 0.10         | 0.81            | -0.63         | 0.84                               | -0.04           | 0.62  | -0.81        | -0.79         |
| HSP70                        | -0.49            |       | -0.60 | -0.18        | -0.36           | 0.78          | -0.41                              | 0.25            | -0.14 | 0.39         | 0.42          |
| LDH                          | 0.71             | -0.60 |       | 0.34         | 0.48            | -0.55         | 0.72                               | 0.00            | 0.58  | -0.75        | -0.76         |
| Lactate                      | 0.10             | -0.18 | 0.34  |              | 0.04            | -0.16         | 0.18                               | 0.76            | 0.30  | -0.53        | -0.23         |
| Peroxidase                   | 0.81             | -0.36 | 0.48  | 0.04         |                 | -0.27         | 0.39                               | 0.22            | 0.62  | -0.46        | -0.39         |
| Catalase                     | -0.63            | 0.78  | -0.55 | -0.16        | -0.27           |               | -0.71                              | 0.37            | -0.05 | 0.55         | 0.49          |
| Glutathione<br>S-transferase | 0.84             | -0.41 | 0.72  | 0.18         | 0.39            | -0.71         |                                    | -0.23           | 0.33  | -0.87        | -0.84         |
| L-Arginine                   | -0.04            | 0.25  | 0.00  | 0.76         | 0.22            | 0.37          | -0.23                              |                 | 0.47  | -0.22        | 0.04          |
| PLA                          | 0.62             | -0.14 | 0.58  | 0.30         | 0.62            | -0.05         | 0.33                               | 0.47            |       | -0.62        | -0.65         |
| Glucose                      | -0.81            | 0.39  | -0.75 | -0.53        | -0.46           | 0.55          | -0.87                              | -0.22           | -0.62 |              | 0.91          |
| Glycogen                     | -0.79            | 0.42  | -0.76 | -0.23        | -0.39           | 0.49          | -0.84                              | 0.04            | -0.65 | 0.91         |               |
| Schiff Bases                 | 0.14             | -0.17 | -0.04 | 0.17         | 0.17            | -0.09         | 0.11                               | -0.79           | -0.39 | 0.28         | 0.06          |



species under conditions of exposure to non-optimal temperatures as previously stated by Pörtner & Giomi (2013).

Possible reasons for the increasing anaerobic processes could be oxidative stress, which is accompanied by the accumulation of reactive oxygen species (Barata et al., 2005). The elevated activity of peroxidase during the gradual temperature increase and the elevated activity of catalase during the gradual temperature decrease reflect activation of the antioxidative systems and the utilization of emerging reactive oxygen species. The decreased activity of peroxidase during the gradual temperature decrease and the decreased activity of catalase during the gradual temperature increase could indicate activation of homeostatic energy maintenance mechanisms (Blokhina et al., 2003). Thus, these contrasting temperature profiles may represent different thermal optima for the enzymes and their specialization to hypo- and hyperthermia stresses. Glutathione S-transferase plays a key role in the mechanisms for the removal of toxic metabolites from organisms. The increased activity of glutathione S-transferase during the temperature increase indicates effective elimination of the secondary products of lipid peroxidation, such as conjugated dienes and trienes (Fridovich, 1998). The absence of any changes in the content of Schiff's bases, which are the final products of lipid peroxidation, during exposure to a wide range of temperatures, confirmed that the protective activity of glutathione S-transferase was highly efficient.

Correlation analyses demonstrated a close interconnection among the parameters of the cellular and biochemical stress-resistance mechanisms (Table 1). Positive correlations were found between the changes in temperature and the activities of peroxidase ( $r = 0.80$ ,  $P = 0.056$ ) and glutathione S-transferase ( $r = 0.83$ ,  $P = 0.042$ ) and between the concentrations of glucose and glycogen ( $r = 0.91$ ,  $P = 0.00037$ ). Negative correlations were found between the changes in temperature and the glucose concentration ( $r = 0.81$ ,  $P = 0.00076$ ) and between the activity of glutathione S-transferase and the concentrations of glucose ( $r = 0.87$ ,  $P = 0.042$ ) and glycogen ( $r = 0.84$ ,  $P = 0.0026$ ), as well as other parameters.

The results of this study clearly show that the activation of cellular and biochemical stress responses of *L. stagnalis* from Eastern Siberian lakes is affected by the environmental temperature range between 3 and 15°C. It was

demonstrated that exposure of the gastropods to temperatures outside this range resulted in activation of HSP70 synthesis, changes in the activities of antioxidative enzymes and alterations in glycogenic energy metabolism and that these conditions can be considered to be physiologically stressful to the tested gastropods as previously stated by Pörtner (2010). Because *L. stagnalis* is a common species inhabiting a wide range of lakes with temperatures higher than 15°C, we suggest that the limits observed in this study can be considered the result of a local temperature adaption of these Eastern Siberian population. The diversity of temperature adaptation among different populations of *L. stagnalis* contributes to the species' common environmental variation and plasticity, which are strongly reflected at the levels of cellular and biochemical processes and the gastropods' stress responses (Kassahn et al., 2009).

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## SHELL MICROSTRUCTURE OF PROTOBRANCHIA (MOLLUSCA: BIVALVIA): DIVERSITY, NEW MICROSTRUCTURES AND SYSTEMATIC IMPLICATIONS

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### ABSTRACT

The shell microstructure of 30 species belonging to 14 genera and nine families of proto-branchs were newly described using scanning electron microscopy. As a result, 13 microstructures were recognized. The shell microstructural composition of protobranchia is conservative at a superfamily level among the Recent species, whereas this trend is not necessarily apply to that of fossil protobranchs. Greater diversity of the shell microstructure was revealed in protobranchs than previously known. (1) Nuculoidea commonly have outer prismatic and middle/inner nacreous structures. The outer prismatic layer is newly classified into five types in Nuculidae. In particular, the irregular fibrous prismatic structure was first observed in Nuculoidea. The interspecific variability of outer prismatic layers seems to provide crucial criteria for phylogenetic grouping in this superfamily. (2) Nuculanoidea have non-nacreous structures including the homogeneous, fibrous prismatic and fine complex crossed lamellar structures. Sareptidae, which should presumably be reclassified from Nuculoidea to Nuculanoidea also follows this pattern. (3) Manzanelloidea have microstructural components similar to those of Nuculanoidea. These features strongly suggest the shell microstructure of protobranchs provide useful bases for higher systematics.

Key words: Bivalvia, Protobranchia, shell microstructure, nacreous structure, prismatic structure, morphological diversity.

### INTRODUCTION

Protobranchs are considered as possibly the oldest clade of the Bivalvia (e.g., by morphology: Allen, 1983; Zardus, 2002; by molecular phylogeny: Kocot et al., 2011; Smith et al., 2011; Bieler et al., 2014). The first occurrence of protobranchs dates back at least to early Ordovician (Cox et al., 1969) and they have not changed their morphology drastically over time (Morris & Fortey, 1976). Protobranchia comprise four Recent superfamilies and two extincted superfamilies according to the current classification: Nuculoidea (Order Nuculida), Solemyoidea and Manzanelloidea (Order Solemyida) and Nuculanoidea (Order Nuculanida), and Afghanodesmatoidea and Tironuculoidea (Order Afghanodesmatida; extinct) (Bouchet et al., 2010; Huber, 2010; Carter et al., 2011; Coan & Valentich-Scott, 2012; Carter et al., 2015). Protobranchs are united by characters of gill structure, hinge configuration, larval development, foot morphology, respiratory pigments

and modes of feeding and digestion (Zardus, 2002). Nuculoidea and Nuculanoidea share taxodont teeth but generally differ in aspects of shell morphology (Coan et al., 2000; Coan & Valentich-Scott, 2012): the posterior end is short in Nuculoidea and usually elongate in Nuculanoidea. Pallial sinuses indicating the existence of siphons are absent in Nuculoidea but present in several families in Nuculanoidea. Manzanelloidea and Solemyoidea are characterized by a unique feeding habit and chemosynthetic system (e.g., Solemyoidea: Stewart & Cavanaugh, 2006; Manzanelloidea: Oliver & Taylor, 2012). However, they differ in the presence or absence of hinge teeth: Manzanelloidea have few vertical teeth, but Solemyoidea is edentate.

Recent protobranchs encompass about 700 species (Huber, 2010) classified into 53 genera, 12 families and four superfamilies according to World Register of Marine Species (WoRMS: <http://www.marinespecies.org/>). However, their criteria for division are not always evident for all

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included species, because their macroscopic shell morphology is generally simple. Therefore, it is important to increase the number of available characters. For example, Zardus (2002) referred to the shell microstructures of protobranchs as taxonomic characteristics in addition to shell and soft-part characters. Molluscan shells are composed of structural units of calcium carbonate called shell microstructures, and their microstructures are categorized into various types by their crystal form and orientation. Therefore, intensive research on shell microstructure is expected to increase useful morphological characters.

Shell microstructure has long been studied chiefly in paleontology, because it can be potentially preserved in fossils and therefore provide a clue for inference on evolution and phylogeny of the past life. Details of various microstructures have been described in several large monographs (e.g., Bøggild, 1930; Taylor et al., 1969, 1973; Carter, 1990a, b). According to the definitions in Carter (1990a), 40 types of mineralized microstructures are recognized in molluscan shells and periostraca in terms of crystal morphology and mineralogy. This variety in molluscan shell microstructure is much more noticeable compared to hard tissues in other animal phyla and/or subphyla. Similarities of shell microstructures in phylogenetically close taxa have been reported in diverse groups of molluscs (Veneridae: Uozumi & Suzuki, 1981; Shimamoto, 1986; Littorinidae: Taylor & Reid, 1990; Cardiidae: Schneider & Carter, 2001; Patellogastropoda: Fuchigami & Sasaki, 2005; Mytilidae: Génio et al., 2012). Therefore, the investigation of shell microstructures is expected to provide novel systematic characters in protobranchs.

There are several papers describing the shell microstructures of protobranchs as summarized in Sato et al. (2013: table 1). It has been widely accepted that Recent nuculoidean shells are characterized in having the nacreous structure and non-nacreous shells are typical to Recent nukulanoideans (e.g., Coan et al., 2000). However, several nacre-bearing fossil nuculoideans were recognized (Carter, 1990a; Carter et al., 2015). For example, the family Polidevciidae, which is the Paleozoic nukulanoidean, has nacreous shell (Carter et al., 2015). Also, several fossil nuculoideans without nacreous structure are reported (subfamily Palaeonuculinae; Carter, 2001). These knowledge suggests the shell microstructure of protobranchs contains a wide range of variations. In solemyids, uniquely formed prismatic structure, the radially elon-

gate simple prismatic structure was found in *Solemya* (e.g., Carter, 1990a, b). Sato et al. (2013) added data on more diverse groups of solemyids in detail. We examined the shell microstructures of Nuculoidea, Nukulanoidea and Manzanelloidea to fill gaps in knowledge in protobranchs in this study.

## MATERIALS AND METHODS

### Material

To evaluate interspecific variations in shell microstructures as widely as possible in protobranchs, a total of 30 species were examined in this study (Figs. 1–229). This taxon sampling covers 9 of 12 known families and 14 of 53 genera of living protobranchs. Several specimens were used for a single species in order to confirm the presence or absence of intraspecific variations in shell microstructure. Samples were collected during KT11-14 of R/V Tansei-Marui (Japan Agency for Marine-Earth Science and Technology: JAMSTEC), KH14-2 of R/V Hakuho-Marui (JAMSTEC), and N365 of R/V Nagasaki-Marui (Nagasaki University), and also during routine dredge surveys of Misaki Marine Biological Station, University of Tokyo. Locality data and registration numbers of voucher specimens are listed in Table 1. All materials in this study are deposited in the Department of Historical Geology and Paleontology in the University Museum, the University of Tokyo (UMUT).

### Identification

Material examined was identified taxonomically mainly based on Okutani (2000), Higo et al. (2001) and Huber (2010). Some type specimens were observed in National Museum of Nature and Science, Tokyo, to verify species identity by the second author. All scientific names were checked in the WoRMS database (<http://www.marinespecies.org>), differing as follows: *Acila archibenthalis* Okutani, 1964 = *Acila mirabilis* (A. Adams & Reeve, 1850); *Jupiteria gordonis* (Yokoyama, 1920) = *Nukulana gordonis* (Yokoyama, 1920); *Jupiteria kirai* (Habe, 1953) = *Neilonella kirai* Habe, 1953; *Leionucula* Quenstedt, 1930 = *Ennucula* Iredale, 1931; *Leionucula teramachii* (Habe, 1958) = *Ennucula siberutensis* (Thiele & Jaekel, 1931); *Portlandia japonica* (A. Adams & Reeve, 1850) = *Megayoldia japonica* (A. Adams & Reeve, 1850); *Port-*



TABLE 1. The list of specimens used in this study. KT11-14, KH14-2 and N365 indicate cruises of R/V Tansei-Mar, Hakuho-Mar, and Nagasaki-Mar, respectively. All localities except for KH14-2 st. NBD-1 are in Japan.

| Species                                                | Sample No. | Latitude              | Longitude               | Depth (m) | Locality                          | Date          | Figures     |
|--------------------------------------------------------|------------|-----------------------|-------------------------|-----------|-----------------------------------|---------------|-------------|
| Superfamily Nuculoidea                                 |            |                       |                         |           |                                   |               |             |
| Family Nuculidae                                       |            |                       |                         |           |                                   |               |             |
| <i>Acila mirabilis</i><br>(A. Adams & Reeve, 1850)     | RM32227    | 33°34.6'N             | 135°00.0'E              | 556.53    | Off Wakayama, KT11-14, st. 3      | Jun. 5, 2011  | 1           |
| <i>Acila mirabilis</i><br>(A. Adams & Reeve, 1850)     | RM32228    | 33°34.6'N             | 135°00.0'E              | 556.53    | Off Wakayama, KT11-14, st. 3      | Jun. 5, 2011  | 31–49       |
| <i>Acila minutoides</i><br>Kuroda & Habe in Habe, 1958 | RM32229    | -                     | -                       | -         | Off Misaki, Kana-gawa Prefecture  | Jul. 25, 2011 | 2, 50–60    |
| <i>Acila insignis</i><br>(Gould, 1861)                 | RM32230    | 39°20.28'N            | 141°54.56'E             | 15.2      | Otsuchi Bay, Iwate Prefecture     | Sep. 7, 2010  | 3, 61–71    |
| <i>Brevinucula</i> sp.                                 | RM32231    | 28°32.27'N–28°34.15'N | 127°02.28'E–127°02.53'E | 606–610   | Off Amami-Oshima Island, N365, J6 | Nov. 16, 2011 | 4, 72–77    |
| <i>Ennucula niponica</i><br>(Smith, 1885)              | RM32232    | 33°34.6'N             | 135°00.0'E              | 556.53    | Off Wakayama, KT11-14, st. 3      | Jun. 5, 2011  | 5           |
| <i>Ennucula niponica</i><br>(Smith, 1885)              | RM32233    | 33°34.6'N             | 135°00.0'E              | 556.53    | Off Wakayama, KT11-14, st. 3      | Jun. 5, 2011  | 78–89       |
| <i>Ennucula siberutensis</i> (Thiele & Jaeckel, 1931)  | RM32234    | 32°22.15'N–32°23.35'N | 129°02.41'E–129°03.05'E | 304–310   | Kasayama Bank, N365, A3           | Nov. 19, 2012 | 6, 90–94    |
| <i>Ennucula tenuis</i><br>(Montagu, 1808)              | RM32235    | 32°09.07'N–32°09.02'N | 128°59.03'E–129°00.45'E | 508–514   | Okikasayama Bank, N365, C5        | Nov. 19, 2012 | 7           |
| <i>Ennucula tenuis</i><br>(Montagu, 1808)              | RM32236    | 28°32.27'N–28°34.15'N | 127°02.28'E–127°02.53'E | 606–610   | Off Amami-Oshima Island, N365, J6 | Nov. 16, 2012 | 95–103      |
| <i>Ennucula</i> sp. 1                                  | RM32237    | 28°33.89'N–28°32.96'N | 127°02.62'E–127°02.20'E | 610–611   | Off Amami-Oshima, N365, J6        | Nov. 16, 2012 | 8, 104–107  |
| <i>Ennucula</i> sp. 2                                  | RM32238    | -                     | -                       | -         | Off Misaki, Kana-gawa Prefecture  | Oct. 27, 2011 | 9, 108–111  |
| <i>Nucula</i> sp.                                      | RM32239    | 33°31.8'N             | 134°59.3'E              | 998.92    | Off Wakayama, KT11-14, st. 4      | Jun. 5, 2011  | 10, 112–117 |
| <i>Nucula gemmulata</i><br>Habe, 1953                  | RM32240    | 32°09.07'N–32°09.02'N | 128°59.03'E–129°00.45'E | 508–514   | Okikasayama Bank, N365, C5        | Nov. 19, 2012 | 11, 118–123 |
| Family Sareptidae                                      |            |                       |                         |           |                                   |               |             |
| <i>Sarepta speciosa</i><br>A. Adams, 1860              | RM32241    | 35°07.90'N–35°08.09'N | 139°34.11'E–139°33.86'E | 95.0–96.2 | Off Misaki, Kana-gawa Prefecture  | Apr. 25, 2012 | 12, 124–134 |
| <i>Setigloma japonica</i><br>(Smith, 1885)             | RM32242    | 47°00.22'N–47°00.91'N | 160°02.62'E–160°01.29'E | 5179–5223 | Off Kamchatka, KH-14-2, st. NBD-1 | May 27, 2014  | 13          |
| <i>Setigloma japonica</i><br>(Smith, 1885)             | RM32243    | 47°00.22'N–47°00.91'N | 160°02.62'E–160°01.29'E | 5179–5223 | Off Kamchatka, KH-14-2, st. NBD-1 | May 27, 2014  | 135–140     |

(continues)



(continued)

| Species                                                                 | Sample No. | Latitude                  | Longitude                   | Depth (m)     | Locality                                  | Date                      | Figures         |
|-------------------------------------------------------------------------|------------|---------------------------|-----------------------------|---------------|-------------------------------------------|---------------------------|-----------------|
| Superfamily Manzanelloidea                                              |            |                           |                             |               |                                           |                           |                 |
| Family Nucinellidae                                                     |            |                           |                             |               |                                           |                           |                 |
| <i>Huxleyia sulcata</i><br>Adams, 1860                                  | RM32244    | 35°07.19'N–<br>35°06.86'N | 139°34.10'E–<br>139°33.75'E | 210–345       | Off Misaki, Kana-<br>gawa Prefecture      | Mar. 14, 14,<br>2012      | 141–<br>145     |
| Superfamily Nuculanoidea                                                |            |                           |                             |               |                                           |                           |                 |
| Family Nuculanidae                                                      |            |                           |                             |               |                                           |                           |                 |
| <i>Nuculana</i> cf.<br><i>soyoae</i><br>Habe, 1958                      | RM32245    | 35°07.21'N                | 139°33.93'E                 | 250           | Off Misaki,<br>Kanagawa<br>Prefecture     | Oct. 24, 15,<br>2011      | 146–<br>154     |
| <i>Nuculana</i><br><i>tanseimaruae</i><br>Tsuchida & Oku-<br>tani, 1985 | RM32246    | 33°34.6'N                 | 135°00.0'E                  | 556.53        | Off Wakayama,<br>KT11-14, st. 3           | Jun. 5,<br>2011           | 16              |
| <i>Nuculana</i><br><i>tanseimaruae</i><br>Tsuchida & Oku-<br>tani, 1985 | RM32247    | 33°34.6'N                 | 135°00.0'E                  | 556.53        | Off Wakayama,<br>KT11-14, st. 3           | Jun. 5,<br>2011           | 155–159         |
| <i>Nuculana acinacea</i><br>Habe, 1958                                  | RM32248    | 32°22.15'N–<br>32°23.35'N | 129°02.42'E–<br>129°03.05'E | 304–310       | Kasayama Bank,<br>N365, A3                | Nov. 19, 17,<br>2012      | 160–<br>163     |
| <i>Nuculana yokoyamai</i><br>Kuroda, 1934                               | RM32249    | -                         | -                           | -             | Off Misaki, Kana-<br>gawa Prefecture      | Mar. 14, 18,<br>2012      | 164–<br>167     |
| <i>Nuculana gordonis</i><br>(Yokoyama, 1920)                            | RM32250    | -                         | -                           | -             | Off Misaki, Kana-<br>gawa Prefecture      | Jul. 25,<br>2011          | 19, 168–<br>172 |
| Family Bathyspinulidae                                                  |            |                           |                             |               |                                           |                           |                 |
| <i>Bathyspinula</i><br><i>calcarella</i><br>(Dall, 1908)                | RM32251    | 47°00.22'N–<br>47°00.91'N | 160°02.62'E–<br>160°01.29'E | 5179–<br>5223 | Off Kamchatka,<br>KH-14-2, st.<br>NBD-1   | May 27, 20,<br>2014       | 173–<br>178     |
| Family Malletiidae                                                      |            |                           |                             |               |                                           |                           |                 |
| <i>Malletia takaii</i><br>Okutani, 1968                                 | RM32252    | 33°31.8'N                 | 134°59.3'E                  | 998.92        | Off Wakayama,<br>KT11-14, st. 4           | Jun. 5,<br>2011           | 21, 179–<br>184 |
| <i>Malletia humilior</i><br>Prashad, 1932                               | RM32253    | 28°33.89'N–<br>28°32.96'N | 127°02.62'E–<br>127°02.20'E | 610–611       | Off Amami-Os-<br>hima, N365               | Nov. 16, 22,<br>2012      |                 |
| <i>Malletia humilior</i><br>Prashad, 1932                               | RM32254    | 28°33.89'N–<br>28°32.96'N | 127°02.62'E–<br>127°02.20'E | 610–611       | Off Amami-Os-<br>hima, N365, J6           | Nov. 16, 185–189,<br>2012 |                 |
| Family Neilonellidae                                                    |            |                           |                             |               |                                           |                           |                 |
| <i>Neilonella soyoae</i><br>Habe, 1958                                  | RM32255    | 33°34.6'N                 | 135°00.0'E                  | 556.53        | Off Wakayama,<br>KT11-14                  | Jun. 5,<br>2011           | 23, 190–<br>196 |
| <i>Neilonella dubia</i><br>Prashad, 1932                                | RM32256    | 28°32.27'N–<br>28°34.15'N | 127°02.28'E–<br>127°02.53'E | 606–610       | Off Amami-Os-<br>hima Island,<br>N365, J6 | Nov. 16, 24,<br>2012      |                 |
| <i>Neilonella dubia</i><br>Prashad, 1932                                | RM32257    | 33°34.6'N                 | 135°00.0'E                  | 556.53        | Off Wakayama,<br>KT11-14, st. 3           | Jun. 5,<br>2011           | 197–200         |
| <i>Neilonella kirai</i><br>Habe, 1953                                   | RM32258    | 32°16.98'N–<br>32°17.23'N | 129°02.99'E–<br>129°04.67'E | 384–378       | West Sanpo<br>Sone, N365, B4              | Nov. 19, 25,<br>2012      | 201–<br>205     |

(continues)



(continued)

| Species                                                                    | Sample No. | Latitude                  | Longitude                   | Depth (m) | Locality                                  | Date                          | Figures |
|----------------------------------------------------------------------------|------------|---------------------------|-----------------------------|-----------|-------------------------------------------|-------------------------------|---------|
| Family Tindariidae                                                         |            |                           |                             |           |                                           |                               |         |
| <i>Tindaria soyoae</i><br>Habe, 1953                                       | RM32259    | 28°32.27'N–<br>28°34.15'N | 127°02.28'E–<br>127°02.53'E | 606–610   | Off Amami-Os-<br>hima Island,<br>N365, J6 | Nov. 16, 26, 206–<br>2012 209 |         |
| Family Yoldiidae                                                           |            |                           |                             |           |                                           |                               |         |
| <i>Megayoldia lischkei</i><br>(Smith, 1885)                                | RM32260    | -                         | -                           | -         | Off Misaki,<br>Kanagawa<br>Prefecture     | Mar. 14, 27, 210–<br>2012 215 |         |
| <i>Megayoldia</i> cf. <i>ja-<br/>ponica</i><br>(A. Adams &<br>Reeve, 1850) | RM32261    | 32°16.98'N–<br>32°17.23'N | 129°02.99'E–<br>129°04.67'E | 384–378   | West Sanpo<br>Sone, N365, B4              | Nov. 19, 28, 216–<br>2012 219 |         |
| <i>Yoldia seminuda</i><br>Dall, 1871                                       | RM32262    | 43°06.68'N–<br>43°06.61'N | 145°45.67'E–<br>145°45.40'E | 94–95     | Off Nemuro<br>Peninsula, Hok-<br>kaido    | Apr. 26, 29, 220–<br>2011 223 |         |
| <i>Yoldia notabilis</i><br>Yokoyama, 1922                                  | RM32263    | 39°20.22'N                | 141°54.21'E                 | 10        | Otsuchi Bay,<br>Iwate Prefecture          | Sep. 7, 30, 224–<br>2010 229  |         |

*landia lischkei* (Smith, 1885) = *Megayoldia lischkei* (Smith, 1885); *Pristigloma japonica* (Smith, 1885) = *Setigloma japonica* (Smith, 1885); *Pseudomalletia* Fischer, 1886 = *Malletia* Desmoulins, 1832; *Spinula oceanica* Filatova, 1958 = *Bathyspinula calcarella* (Dall, 1908); *Yoldia johanni* Dall, 1925 = *Yoldia seminuda* Dall, 1871.

Observations of Shell Microstructures

To characterize all shell microstructures of protobranchs, fractured and polished planes were observed in radial, transverse and horizontal sections with scanning electron microscopes (SEM: Keyence-VE8800, Hitachi-S2250N and Hitachi-S4500) at UMUT. Polished planes were filled with epoxy resin (S-31, Devcon Corp.) prior to cutting. The polished planes or fractured fragments were treated by one of the following methods: (1) etching with 0.2% HCl for 1–30 minutes, (2) removal of organic materials with sodium hypochlorite for 10–120 minutes, (3) etching with 0.2% HCl for 1–5 minutes after immersion in sodium hypochlorite for 30 minutes, or (4) non-chemical treatment. After cleaning with an ultrasonic cleaner, the samples were coated with platinum vanadium or osmium tetroxide for observations with SEM.

The components of the shell layers and shell microstructures of each layer are described by taxa (Figs. 1–229) and summarized in Figures 230–237 and Tables 2 and 3. Terminology for the shell microstructure was based on Carter (1990a) and Carter et al. (2012), and new terms were proposed for newly found types of microstructure.

Abbreviations

|       |                                                       |
|-------|-------------------------------------------------------|
| CN    | columnar nacreous structure                           |
| CP    | composite prismatic structure                         |
| DCP   | denticular composite prismatic structure              |
| fCCL  | fine complex crossed lamellar structure               |
| FP    | fibrous prismatic structure                           |
| Hom   | homogeneous structure                                 |
| ISP   | irregular simple prismatic structure                  |
| ISphP | irregular spherulitic prismatic structure             |
| IFP   | irregular fibrous prismatic structure                 |
| INDCP | irregular nondenticular composite prismatic structure |
| N     | nacreous structure                                    |
| NDCP  | nondenticular composite prismatic structure           |
| SN    | sheet nacreous structure                              |
| Sph   | spherulitic structure                                 |



RESULTS

Superfamily Nuculoidea  
Family Nuculidae  
*Acila mirabilis*  
(A. Adams & Reeve, 1850)  
(Figs. 1, 31–49)

*Shell Layers:* The outer, middle, myostracum and inner layers are present (Figs. 31–49). Both middle and inner layers are divided by the myostracum. The outer and middle layers thicken ventrally. The inner layer lies dorsal to the pallial line and also thickens dorsally, whereas the thickest part is distributed in the middle part of a radial section. The myostracum thickens ventrally with growth. However, it becomes thinner subsequently and nearly disappears in the ventral part. The shell is up to approximately 550 μm thick in the observed specimen. The middle part of shell is the thickest.

*Outer Layer:* Irregular nondenticular composite prismatic structure (INDCP, new name; Figs. 33–35; for type of prismatic structures: Table 2). The outer layer consists of acicular crystals; it is approximately 3 μm in diameter and 30 μm long (Fig. 33). These crystals recline at angles of approximately 10–80° against the growth direction in a radial section and compose the first-order prisms weakly radiating toward the depositional surface (Figs. 34, 35). The average width of the first-order prisms is approximately 10 μm.

*Middle Layer:* Columnar nacreous structure (Figs. 36–38). Nearly polygonal tablets stack vertically on the exterior side, but gradually shift to irregularly stacked sheet nacre toward the shell interior. At the innermost part of the middle layer, they pile up like a brick wall and are hardly distinguishable from the inner layer, which consists of a sheet nacreous structure (Figs. 41, 42). Nacre columns stack on a tilt parallel to the long axes of acicular crystals

TABLE 2. The characterization of the types of prismatic structure in nuculids.

| Type                              | First-order structure                                                                                                                                      | Second-order structure                                                               | Species                                         |
|-----------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------|-------------------------------------------------|
| ISphP                             | Consisting of acicular crystals weakly radiating to depositional surface or aligned in parallel from an initial spherulite , spindle, or single of origin. | Long acicular crystals (high length/ width ratio)                                    | <i>A. minutoides</i> ,<br><i>Ennucula</i> sp. 2 |
| IFP <i>sensu</i><br>Carter (1990) | Consisting of acicular crystals showing nodular subunits along their length                                                                                | Long acicular crystals (high length/ width ratio)                                    | <i>Acila insignis</i>                           |
| IFP type-A<br>(new name)          | Consisting of acicular crystals deeply slanting against growth direction exterior and shallowly slanting interior                                          | Thin acicular crystals (outer sublayer) and thick acicular crystals (inner sublayer) | <i>Brevinucula</i><br>sp.                       |
| IFP type-B<br>(new name)          | Consisting acicular crystals slanting at deep angle against growth direction at outer part and bent to growth direction                                    | L-shaped acicular crystals                                                           | <i>E. siberutensis</i> , <i>E.</i> sp. 1        |
| DCP                               | Consisting of acicular crystals spreading like fan ventrally with dentateline boundary                                                                     | Long acicular crystals (high length/ width ratio)                                    | <i>Nucula gemmulata</i> , <i>N.</i> sp.         |
| NDCP                              | Consisting of acicular crystals weakly radiating to depositional surface or aligned in parallel, without dentateline boudary                               | Short acicular crystals (low length/ width ratio)                                    | <i>E. tenuis</i> , <i>E. niponica</i>           |
| INDCP<br>(new name)               | NDCP with rather narrow first-order prisms with irregular, vertically elongate cross-section shapes                                                        | Long acicular crystals (high length/ width ratio)                                    | <i>A. mirabilis</i>                             |



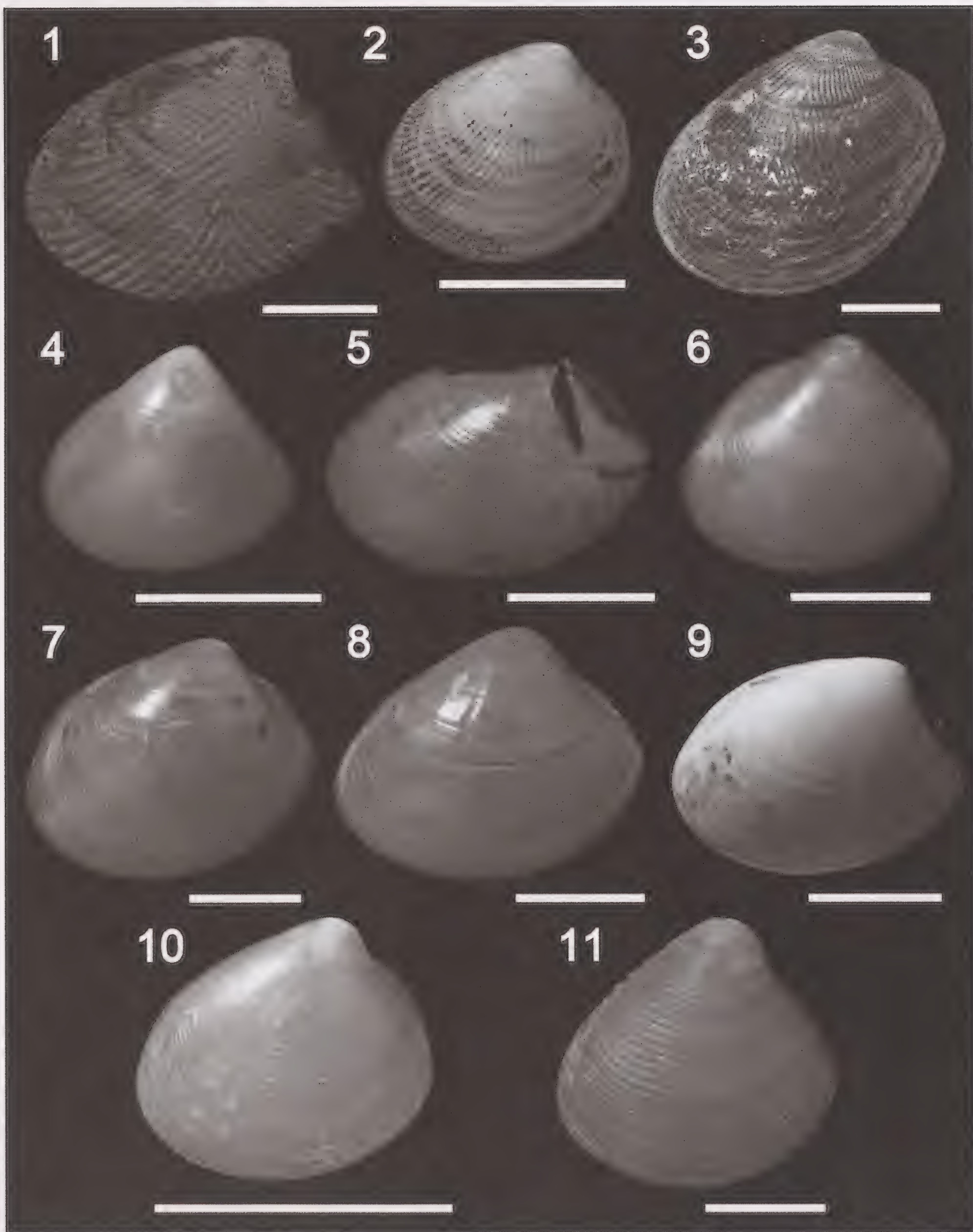
of the outer layer at the outermost part of the middle layer and nearly vertically at the innermost part. While each tablet connects to the next tablet in a narrow sense (Fig. 38), the width of each assumed tablets is around 6  $\mu\text{m}$ . Thickness of the tablets is approximately 1  $\mu\text{m}$  at the outer part of the middle layer; it reduced inward, reaching 0.3  $\mu\text{m}$ . Nacre tablets grow spirally (Fig. 38). Homogeneous structure is recognized at growth lines (Figs. 43, 44).

*Myostracum*: Irregular simple prismatic and homogeneous structures (Figs. 41, 42, 46–49). At the most thickened part, irregularly shaped acicular crystals, which are around 5  $\mu\text{m}$  long in the long axes, compose the myostracum (Fig. 42). At the thinned part, irregularly shaped blocky crystals, which are sort of false nacre tablets, compose the myostracum. Only nano-scaled granular crystals are distributed between nacre tab-

TABLE 3. List of shell microstructures observed in this study (\*Outer sublayer of outer layer, \*\*Inner sublayer of outer layer).

| Family          | Species                               | Outer layer | Middle layer | Myostracum  | Inner layer |
|-----------------|---------------------------------------|-------------|--------------|-------------|-------------|
| Nuculidae       | <i>Acila mirabilis</i>                | INDCP       | CN           | ISP, Hom    | SN          |
|                 | <i>Acia minutoides</i>                | ISphP       | CN           | blocky      | SN          |
|                 | <i>Acila insignis</i>                 | IFP         | CN           | Hom         | SN          |
|                 | <i>Brevinucula</i> sp.                | IFP type-A  | SN           | blocky, ISP | SN          |
|                 | <i>Ennucula niponica</i>              | NDCP        | CN           | blocky, ISP | SN          |
|                 | <i>Ennucula siberutensis</i>          | IFP type-B  | SN           | -           | SN          |
|                 | <i>Ennucula tenuis</i>                | NDCP        | CN           | ISP         | SN          |
|                 | <i>Ennucula</i> sp. 1                 | IFP type-B  | CN           | Hom         | SN          |
|                 | <i>Ennucula</i> sp. 2                 | ISphP       | CN           | -           | SN          |
|                 | <i>Nucula</i> sp.                     | DCP         | SN           | ISP         | SN          |
|                 | <i>Nucula gemmulata</i>               | DCP         | weakly CN    | blocky      | SN          |
| Sareptidae      | <i>Sarepta speciosa</i>               | Hom, fCCL   | -            | ISP         | Hom         |
|                 | <i>Setigloma japonica</i>             | fCCL        | -            | ISP         | fCCL        |
| Manzanellidae   | <i>Huxleyia sulcata</i>               | Hom, fCCL   |              |             |             |
| Nuculanidae     | <i>Nuculana</i> cf. <i>soyoae</i>     | Hom, fCCL   | -            | ISP         | Hom         |
|                 | <i>Nuculana tanseimaruae</i>          | FP*         | Hom, fCCL**  | ISP         | Hom         |
|                 | <i>Nuculana acinacea</i>              | Hom         | -            | -           | Hom         |
|                 | <i>Nuculana yokoyamai</i>             | Hom         | -            | -           | Hom         |
|                 | <i>Nuculana gordonis</i>              | FP*         | Hom**        | ISP         | Hom, fCCL   |
| Bathyspinulidae | <i>Bathyspinula calcarella</i>        | FP*         | Hom, fCCL**  | -           | Hom         |
| Malletiidae     | <i>Malletia takaii</i>                | Hom         | -            | ISP         | fCCL        |
|                 | <i>Malletia humilior</i>              | Hom         | -            | ISP         | fCCL        |
| Neilonellidae   | <i>Neilonella soyoae</i>              | FP*         | Hom**        | -           | Hom         |
|                 | <i>Neilonella dubia</i>               | FP*         | Hom**        | ISP         | Hom         |
|                 | <i>Neilonella kirai</i>               | FP*         | Hom**        | ISP         | Hom         |
| Tindariidae     | <i>Tindaria soyoae</i>                | Hom         | -            | ISP         | Hom         |
| Yoldiidae       | <i>Megayoldia lischkei</i>            | Hom, Sph    | -            | ISP         | fCCL        |
|                 | <i>Megayoldia</i> cf. <i>japonica</i> | FP*         | Hom**        | ISP         | Hom, fCCL   |
|                 | <i>Yoldia seminuda</i>                | Hom         | -            | ISP         | fCCL        |
|                 | <i>Yoldia notabilis</i>               | Hom         | -            | ISP         | fCCL        |





FIGS. 1–11. External shell morphology of left valve of Nuculidae examined. FIG. 1: *Acila mirabilis*; FIG. 2: *Acila minutoides*; FIG. 3: *Acila insignis*; FIG. 4: *Brevinucula* sp.; FIG. 5: *Ennucula niponica*; FIG. 6: *Ennucula siberutensis*; FIG. 7: *Ennucula tenuis*; FIG. 8: *Ennucula* sp. 1; FIG. 9: *Ennucula* sp. 2; FIG. 10: *Nucula* sp.; FIG. 11: *Nucula gemmulata*. Scale bars = 5 mm.



lets where the myostracum is thinner (Figs. 41, 46–49). Nacre tablets in the middle layer and granular crystals are distributed at the pallial line and adductor muscle scars in the observed specimen (Figs. 46–49).

*Inner Layer:* Sheet nacreous structure (Figs. 39–42, 46, 47). Nacre tablets are approximately 0.7  $\mu\text{m}$  thick and brick-like. Although the boundary of adjacent tablets is indistinct and fused with each other (Fig. 40), their width is around 4–10  $\mu\text{m}$ . Nacre tablets in

the inner layer show a spiral growth pattern as in the middle layer (Fig. 40).

*Acila minutoides*

Kuroda & Habe in Habe, 1958  
(Figs. 2, 50–60)

*Shell Layers:* Outer, middle, myostracum and inner layers are present (Figs. 50–54). The outer and middle layers thicken ventrally, and the inner layer generally thickens dorsally. The



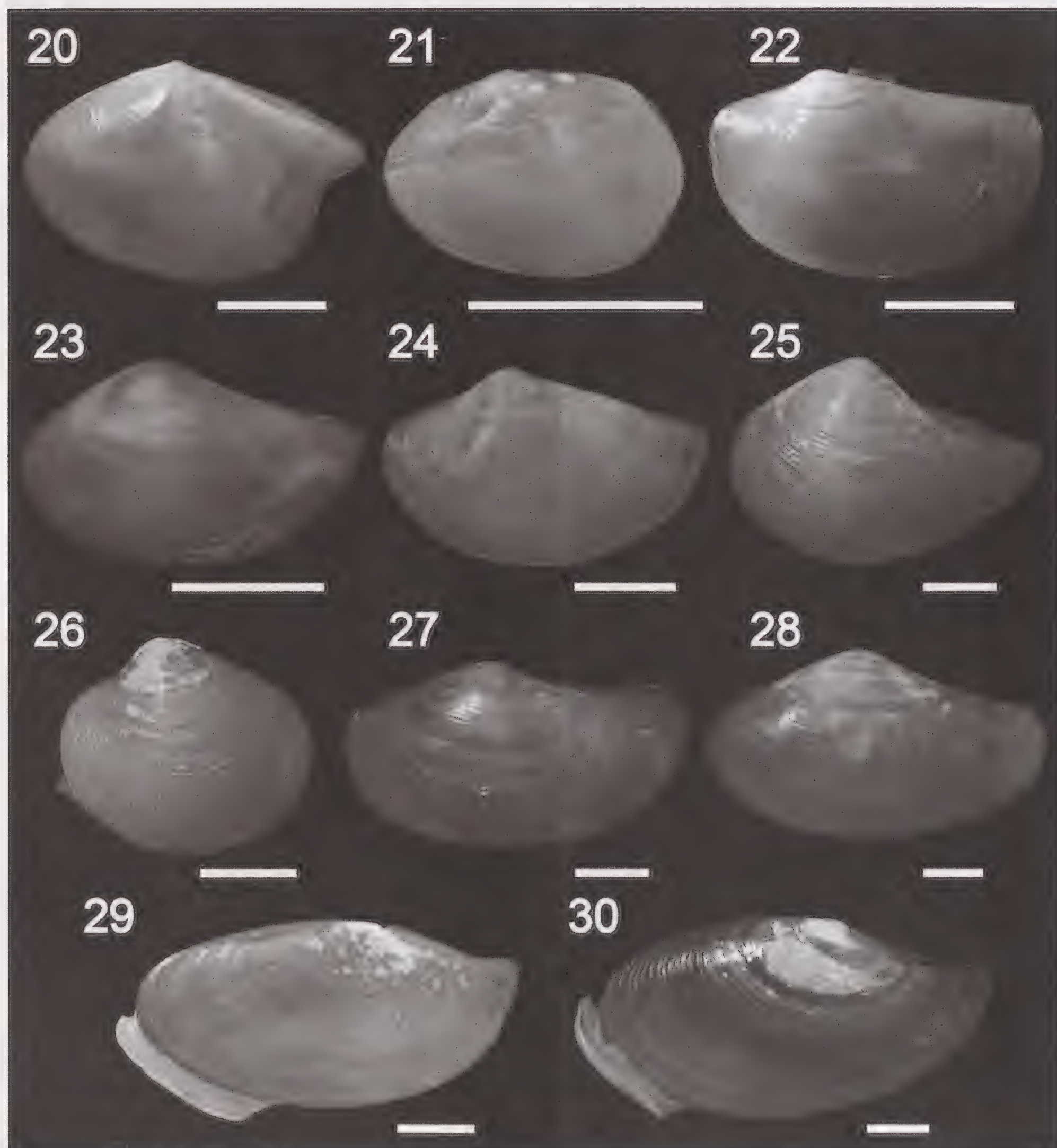
FIGS. 12–19. External shell morphology of left valve of Sareptidae, Nucinellidae and Nuculanidae examined. FIG. 12: *Sarepta speciosa*; FIG. 13: *Setigloma japonica*; FIG. 14: *Huxleyia sulcata*; FIG. 15: *Nuculana* cf. *soyoae*; FIG. 16: *Nuculana tanseimaruae*; FIG. 17: *Nuculana acinacea*; FIG. 18: *Nuculana yokoyamai*; FIG. 19: *Nuculana gordonis*. Figs. 12, 13, 15–19: Scale bars = 5 mm; Fig. 14: Scale bar = 1 mm.



boundary between the middle and inner layers is indistinct at the ventral and dorsal parts due to thinning of the myostracum. The shell thickens at the ventral part and is up to approximately 270  $\mu\text{m}$  thick in the observed specimen.

*Outer Layer:* Irregular spherulitic prismatic (IsphP) structure (Figs. 51–54). The outer

layer consists of acicular crystals up to approximately 2.5  $\mu\text{m}$  in diameter and approaches approximately 22  $\mu\text{m}$  long in the long axis (Figs. 53, 54). These crystals recline at an angle of approximately 40° to 90° against the growth direction in the radial section. Acicular crystals align parallel to nearby crystals



FIGS. 20–30. External shell morphology of left valve of Bathyspinulidae, Malletiidae, Tindariidae and Yoldiidae examined. FIG. 20: *Bathyspinula calcarella*; FIG. 21: *Malletia takaii*; FIG. 22: *Malletia humilior*; FIG. 23: *Neilonella soyoae*; FIG. 24: *Neilonella dubia*; FIG. 25: *Neilonella kirai*; FIG. 26: *Tindaria soyoae*; FIG. 27: *Megayoldia lischkei*; FIG. 28: *Megayoldia cf. japonica*; FIG. 29: *Yoldia seminuda*; FIG. 30: *Yoldia notabilis*. Scale bars = 5 mm.



and do not form the first-order prisms at the thinned part (nearly fibrous prismatic; Fig. 52), and compose the first-order prisms weakly at the thickened part (Figs. 51, 53), weakly radiating toward the depositional surface.

**Middle Layer.** Columnar nacreous structure (Figs. 51, 52, 55, 56). Nacreous tablets weakly stack vertically at the exterior side (columnar nacreous) and are brick-like (sheet nacreous) due to inwards weakening vertical stacking. Nacre tablets are around  $1.5\text{ }\mu\text{m}$  thick at the exterior side (Figs. 55, 56) and become thinner inwards (around  $0.8\text{ }\mu\text{m}$ ; Figs. 59, 60). Although the boundary of adjacent tablets is indistinct due to fusion, the width of individual tablets is around  $3\text{--}10\text{ }\mu\text{m}$ .

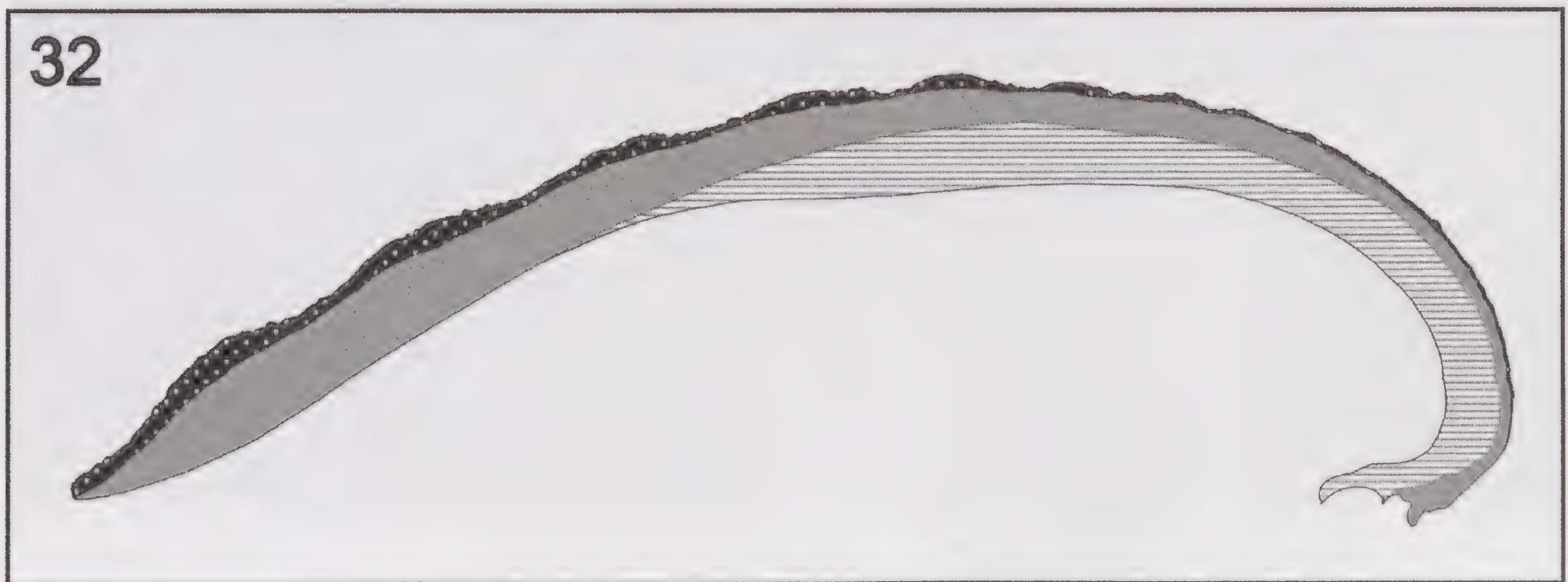
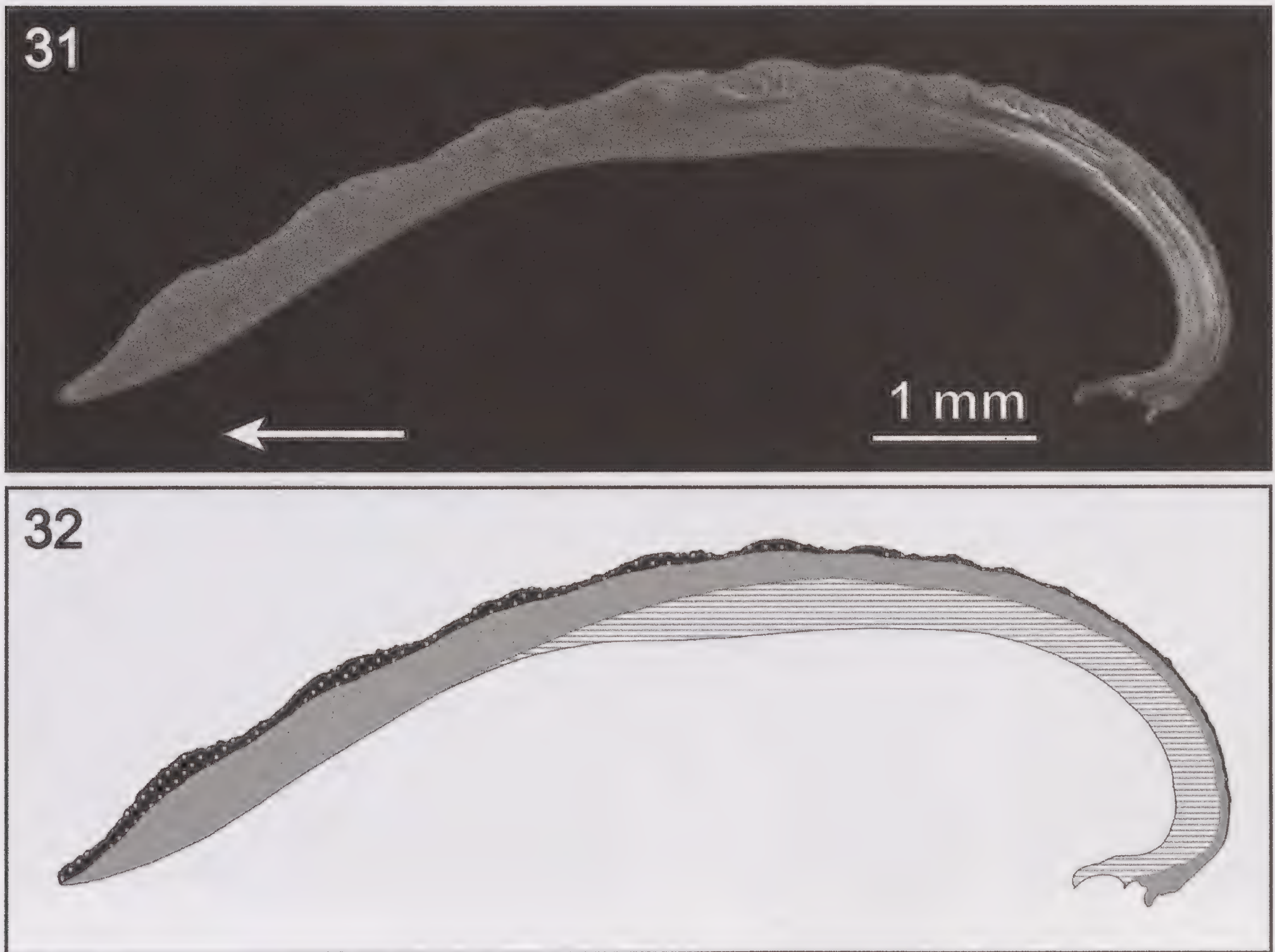
**Myostracum:** This layer consists of irregular blocky crystals or granular crystals (Figs. 59, 60) which are mostly very thin (less than

$1\text{ }\mu\text{m}$ ) and filled with granular crystals (Fig. 59). The most thickened part exhibits irregular blocky crystals (up to  $4\text{ }\mu\text{m}$  thick) (Fig. 60).

**Inner Layer.** Sheet nacreous (Figs. 57–60). Irregular polygonal tablets are approximately  $0.6\text{ }\mu\text{m}$  thick and brick-like. The boundary of adjacent tablets is indistinct and fused with each other. The width of each tablet is around  $2\text{--}7\text{ }\mu\text{m}$ .

*Acila insignis* (Gould, 1861)  
(Figs. 3, 61–71)

**Shell Layers:** Outer, middle, myostracum and inner layers are present (Figs. 61–65). The outer and middle layers thicken ventrally. The inner layer lies dorsal to the pallial line and thickens dorsally, but the thickest part is distributed in the middle of the radial section. The shell is



FIGS. 31, 32. Radial section of observed *Acila mirabilis*. White arrow indicates the growth direction. FIG. 32: Pattern diagram of Fig. 31 showing the distribution of the outer, middle and inner layers. The myostracum, which is distributed in adductor and pallial muscle attachments, is located on the border of the middle and inner layers but not illustrated due to its thinness.

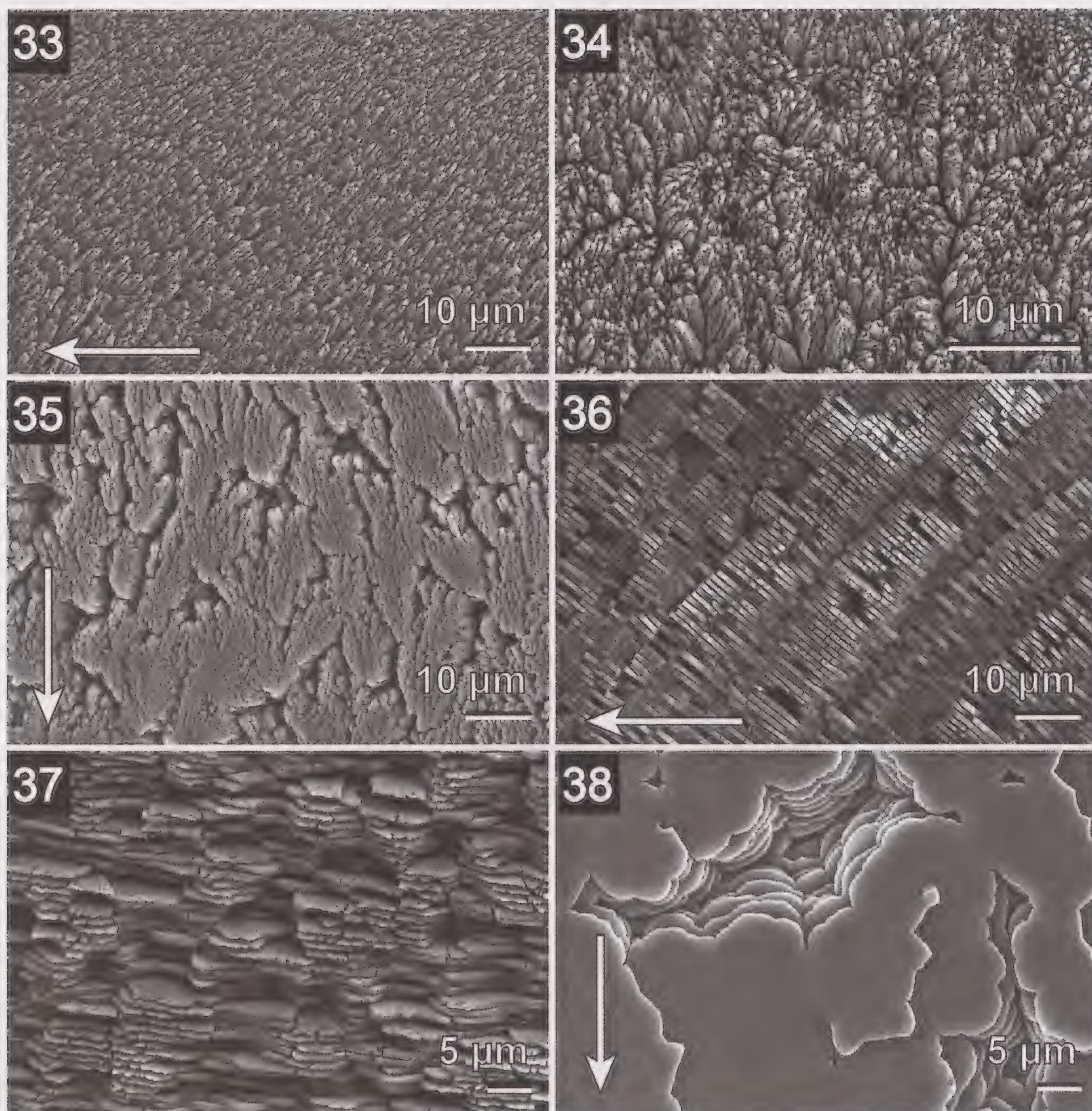


thickened ventrally and is up to approximately 920  $\mu\text{m}$  thick in the observed specimen.

**Outer Layer.** Irregular fibrous prismatic structure of Carter et al. (2012) with minor irregular spherulitic prismatic (ISphP) structure (Figs. 64, 65). The outer layer consist of acicular crystals up to approximately 1  $\mu\text{m}$  in diam-

eter. These crystals recline at an angle of approximately 10–70° against the growth direction in a radial section and compose the first-order prisms weakly radiating toward the depositional surface.

**Middle Layer.** Columnar nacreous structure (Figs. 66–69). Nearly polygonal tablets

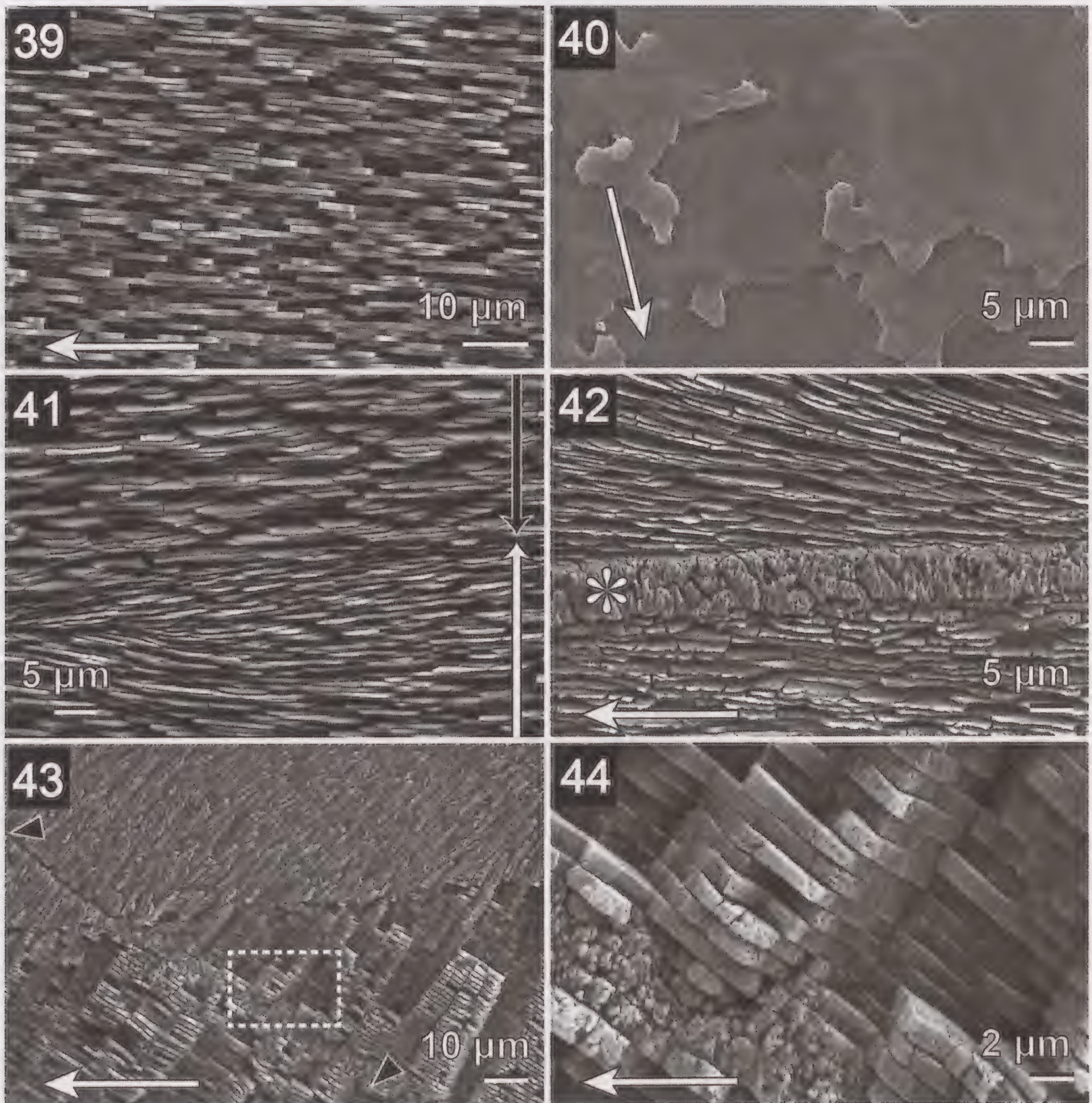


FIGS. 33–38. Scanning electron micrographs of *Acila mirabilis* microstructure. White arrow indicate growth direction. FIG. 33: Radial section of irregular nondenticular composite prismatic structure of the outer layer; FIG. 34: Transverse section of irregular nondenticular composite prismatic structure of the outer layer; FIG. 35: Inner surface of irregular nondenticular composite prismatic structure of the outer layer; FIG. 36: Radial section of columnar nacreous structure of the middle layer; FIG. 37: Transverse section of columnar nacreous structure of the middle layer; FIG. 38: Inner surface of columnar nacreous structure of the middle layer. FIGS. 33, 34, 36, 37: Middle part of shell; FIGS. 35, 38: Ventral part of shell.



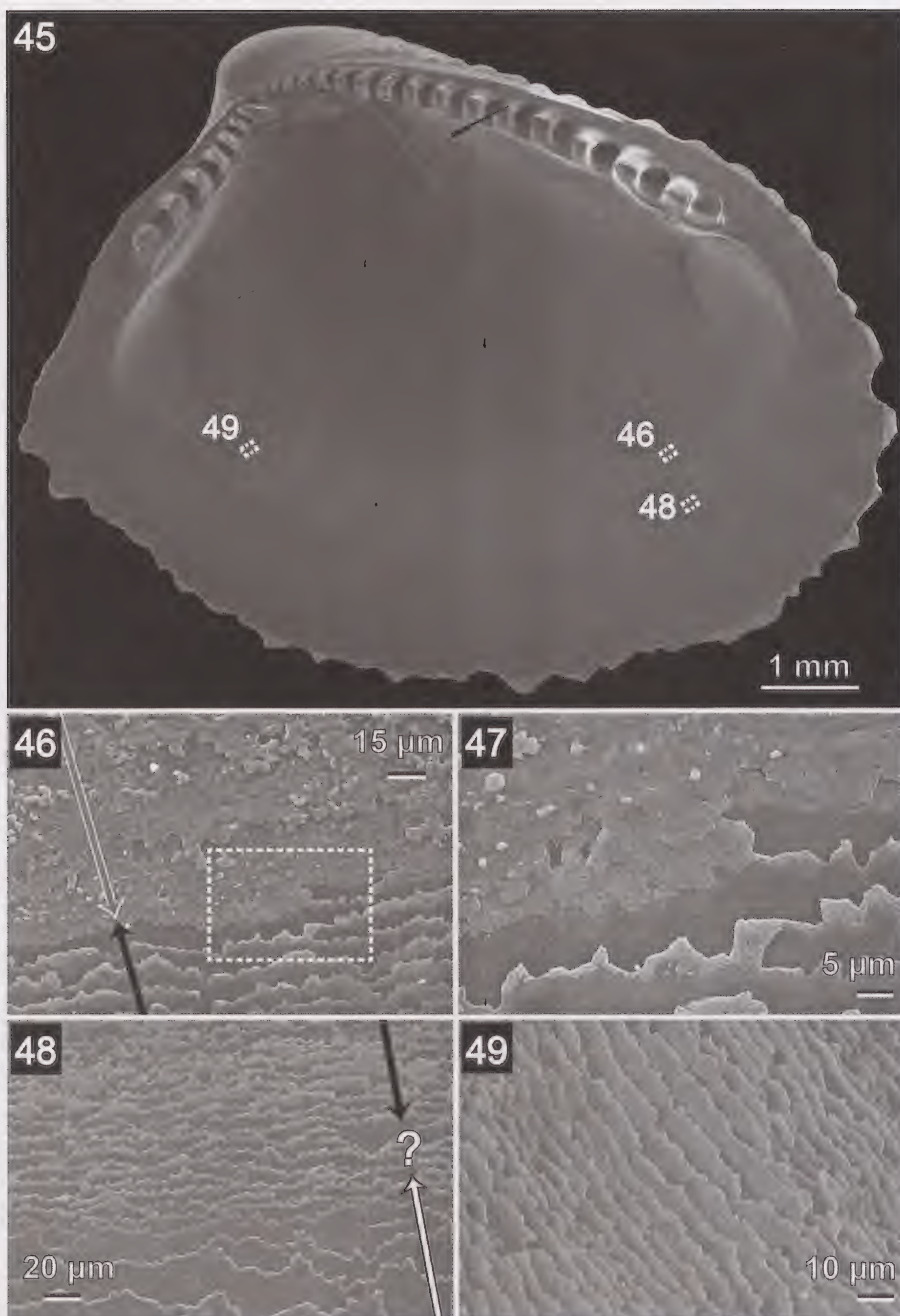
stack vertically in the exterior side (Figs. 66, 67), but gradually shift to irregularly stacked sheet nacre towards the shell interior (Figs. 68, 69). Nacre columns stack on a tilt at the outermost part of the middle layer and near-

ly vertically at its innermost part. Each tablet connects to the adjacent tablets mutually, and the width of each assumed each tablets is approximately 4–7  $\mu\text{m}$ . The thickness of each tablet is approximately 1  $\mu\text{m}$ .



FIGS. 39–44. Scanning electron micrographs of *Acila mirabilis* microstructure. Horizontal white arrow indicate growth direction. FIG. 39: Radial section of sheet nacreous structure of the inner layer; FIG. 40: Inner surface of sheet nacreous of the inner layer; FIG. 41: Transverse section of nacreous structure of the middle and inner layers at ventral part of shell. Black arrow indicates the middle layer and white arrow exhibits the inner layer; FIG. 42: Radial section of nacreous structure of the middle and inner layers at dorsal part of shell. Asterisk indicates the myostracum; FIG. 43: Radial section of the outer and middle layers. Black arrowhead indicates the growth line; FIG. 44: Closer view of broken-lined square in Fig. 43. Homogeneous structure was recognized at the growth line. FIGS. 39, 43, 44: Middle part of shell; FIGS. 40, 41: Ventral part of shell; FIG. 42: Dorsal part of shell.





FIGS. 45–49. Scanning electron micrographs of *Acila mirabilis* microstructure. FIG. 45: Inner surface; FIGS. 46, 48, 49: Closer view of broken-lined square in Fig. 45; FIG. 47: Closer view of broken-lined square in Fig. 46. White arrow, the middle layer; black arrow, the pallial line; gray arrow, the inner layer. Question mark implies indistinct boundary. Nacre tablets and granular crystals are distributed to the pallial line.

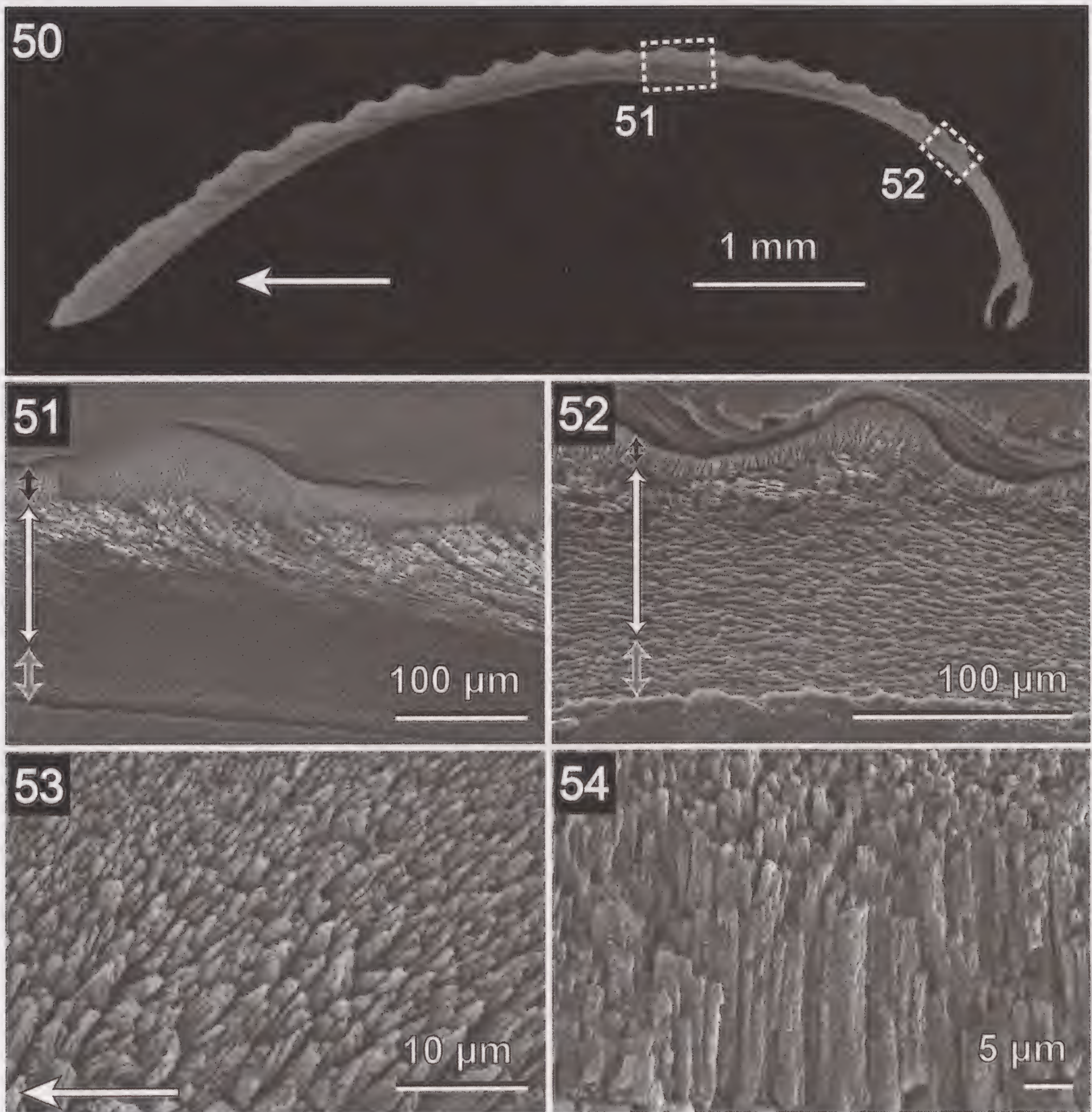


*Myostracum*: Homogeneous structure (Figs. 68, 69). Thickness of this layer reaches approximately 1.5  $\mu\text{m}$ .

*Inner Layer*: Sheet nacreous (Figs. 68–71). Nacre tablets that are approximately 0.5–1.5  $\mu\text{m}$  thick and brick-like. Although the boundary of adjacent tablets is indistinct due to fusion, their width is around 3–8  $\mu\text{m}$ .

*Brevinucula* sp.  
(Figs. 4, 72–77)

*Shell Layers*: Outer, middle, myostracum and inner layers are present (Figs. 72–77). The outer layer has two sublayers. Both sublayers are of fibrous prismatic structure but their angle to the shell surface and width are

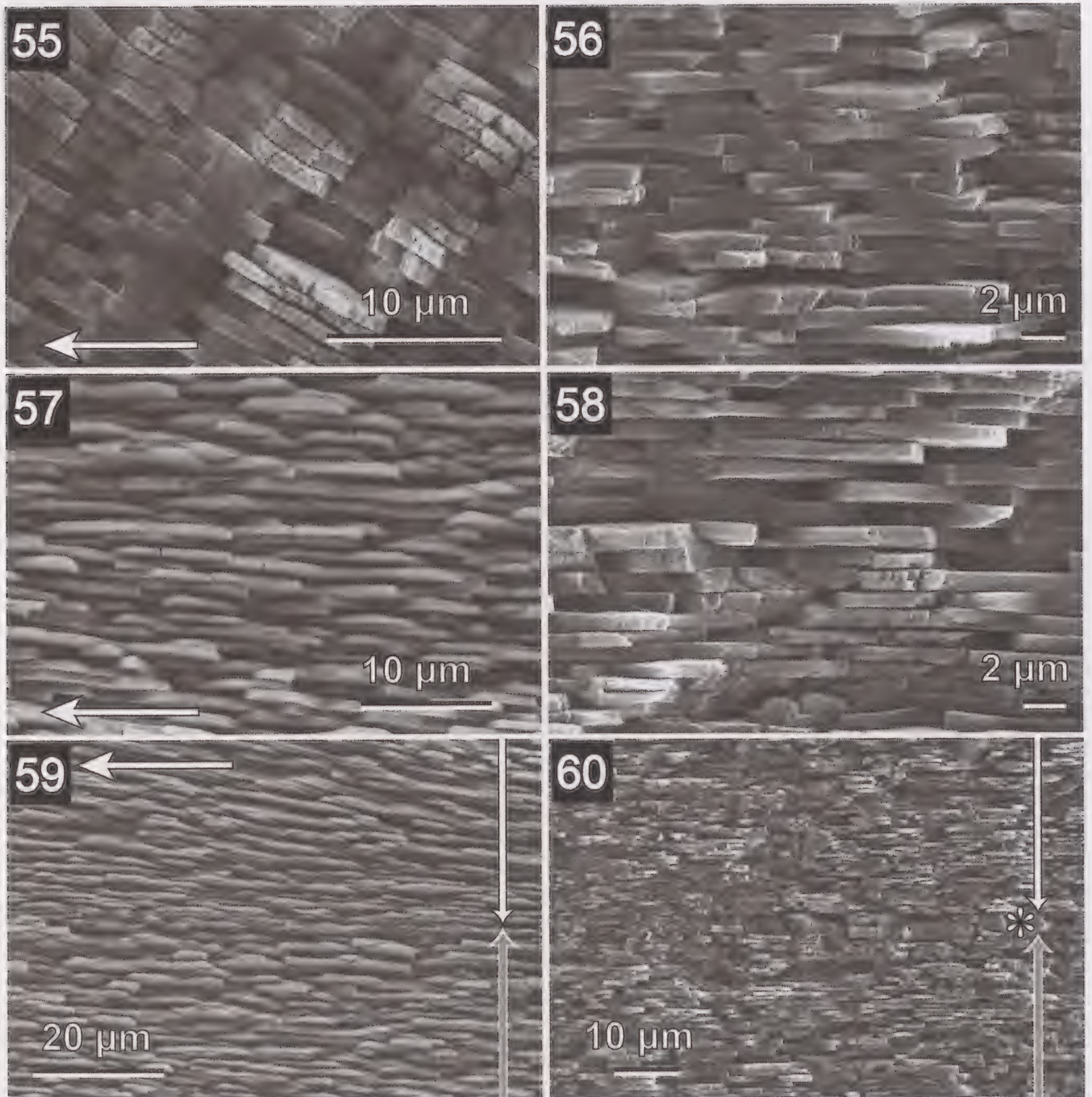


FIGS. 50–54. Scanning electron micrographs of *Acila minutoides* microstructure. White arrow indicate growth direction. FIG. 50: Radial section of shell; FIG. 51: Closer view of broken-lined square in Fig. 50 showing middle part of the shell section. Black arrow, the outer layer; white arrow, the middle layer; gray arrow, the inner layer; FIG. 52: Closer view of broken-lined square in Fig. 50 showing dorsal part of the shell section. Black arrow, the outer layer; white arrow, the middle layer; gray arrow, the inner layer; FIG. 53: Radial section of Irregular spherulitic prismatic structure of the outer layer; FIG. 54: Transverse section of fibrous prismatic structure of the outer layer. FIGS. 53, 54: Middle part of shell.



different. The boundary between the innermost part of the outer layer and outermost part of the middle layer is smooth. The outer and middle layers thicken ventrally, whereas

the myostracum and inner layer thicken dorsally. This species has a relatively thick (approximately 330  $\mu\text{m}$ ) shell for their small shell length.



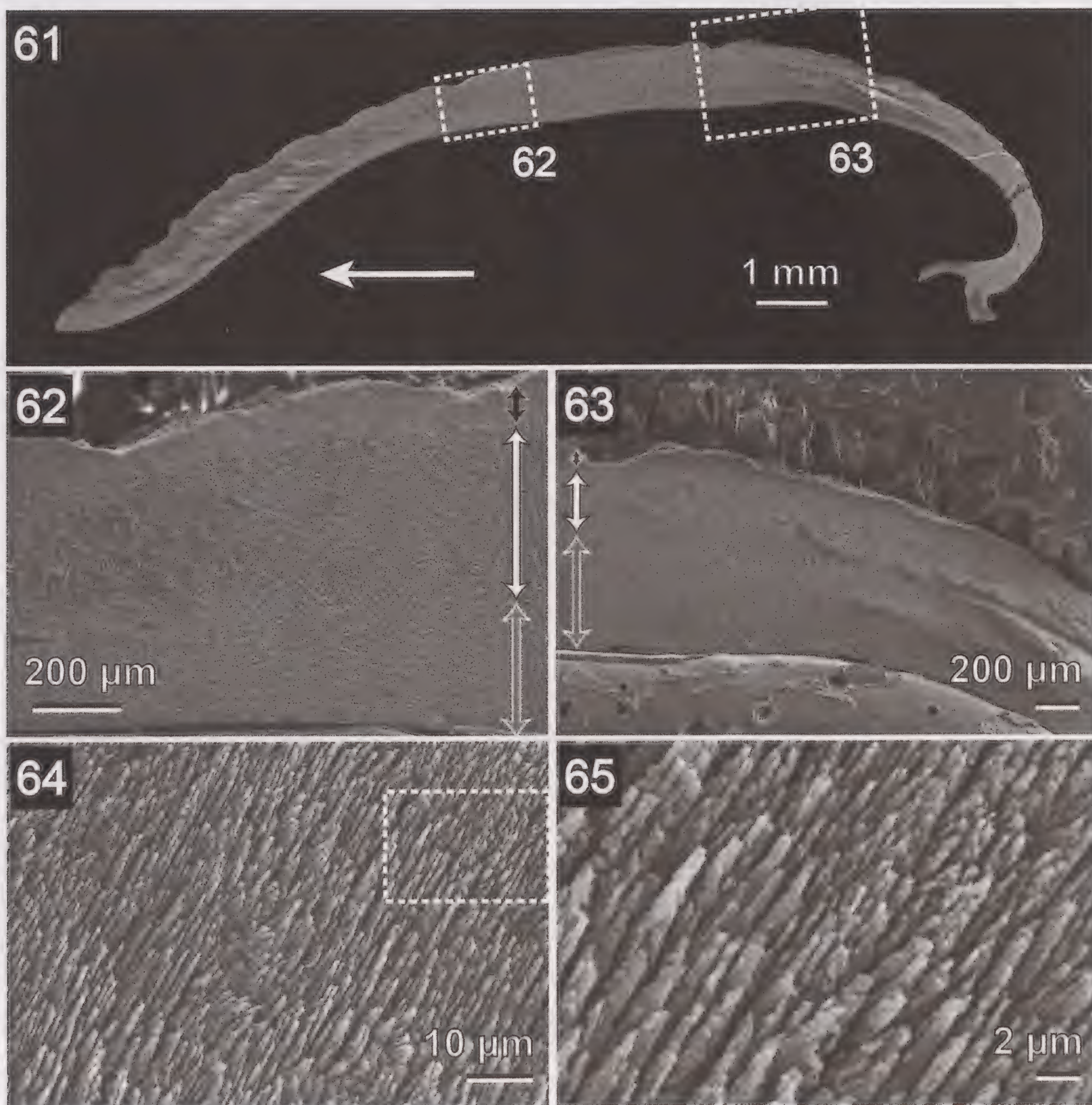
FIGS. 55–60. Scanning electron micrographs of *Acila minutoides* microstructure. Horizontal white arrow indicate growth direction. FIG. 55: Radial section of columnar nacreous structure of the middle layer; FIG. 56: Transverse section of nacreous structure of the middle layer; FIG. 57: Radial section of sheet nacreous structure of the inner layer; FIG. 58: Transverse section of sheet nacreous structure of the inner layer; FIG. 59: Radial section of nacreous structure of the middle and inner layers at ventral part of shell. Myostracum is indistinct. Vertical white arrow indicates the middle layer and gray arrow indicates the inner layer; FIG. 60: Transverse section of nacreous structure of the middle and inner layers at dorsal part of shell. Myostracum is consist of irregular blocky crystals. Vertical white arrow, the middle layer; gray arrow, the inner layer. Asterisk shows the myostracum and white arrow is the inner layer. FIGS. 55–60: Middle part of shell.



*Outer Layer.* Irregular fibrous prismatic structure consisting of two sublayers (IFP type-A, new name; figs. 72, 73). Acicular crystals in the outer sublayer recline at a steep angle of approximately  $60^\circ$  against the growth direction in the radial section but  $15^\circ$  in the inner sublayer. The width of the crystals is approxi-

mately  $0.8\text{--}1.5\text{ }\mu\text{m}$  in the outer sublayer and  $2.5\text{--}40\text{ }\mu\text{m}$  in the inner sublayer.

*Middle Layer.* Sheet nacreous structure (Figs. 73, 74, 76, 77). Nacre tablets are brick-like and stack parallel to the long axes of the acicular crystals of the inner sublayer of the outer layer and nearly vertically at its inner-



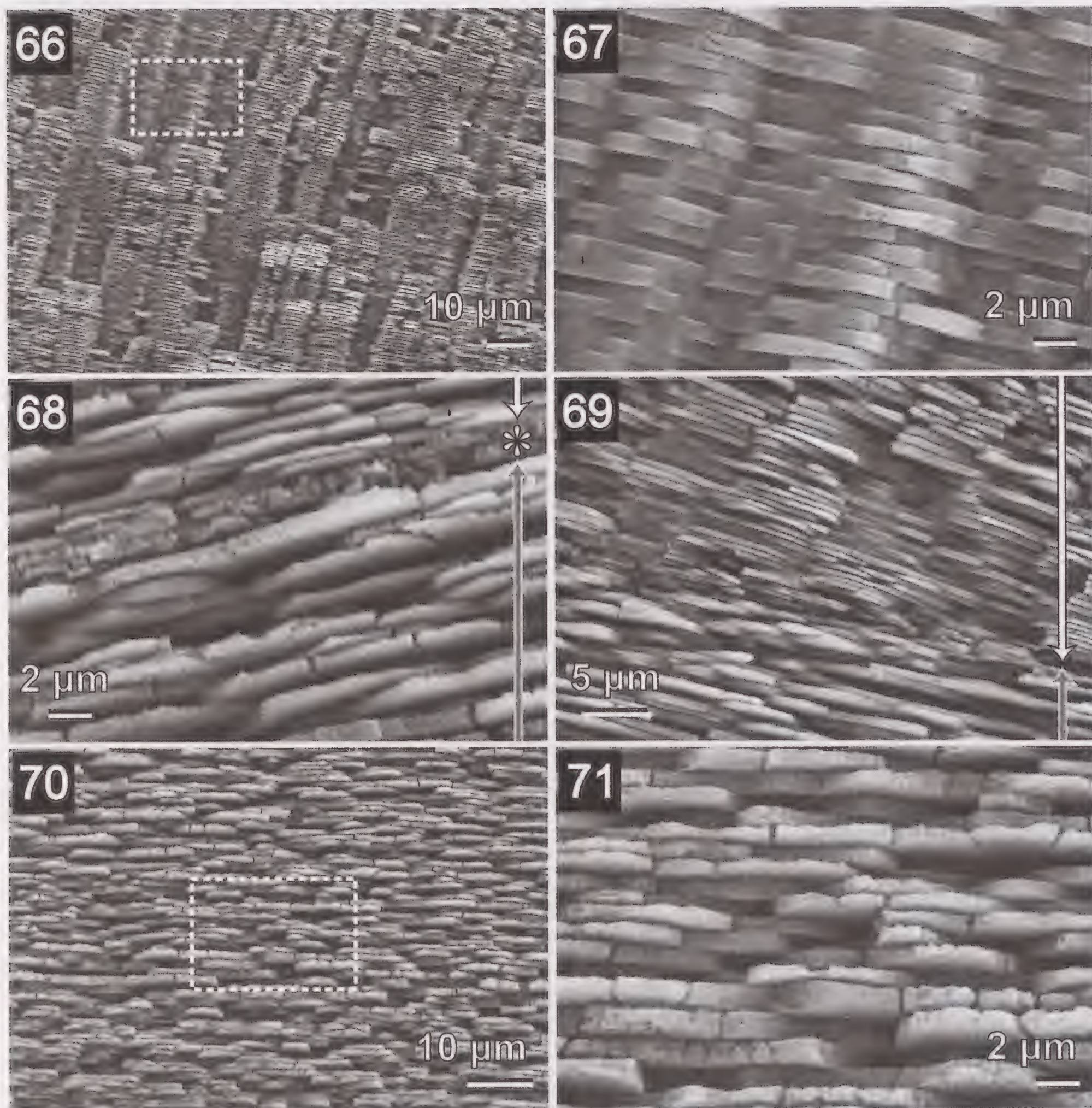
FIGS. 61–65. Scanning electron micrographs of *Acila insignis* microstructure. Horizontal white arrow indicate growth direction. FIG. 61: Radial section of shell; FIG. 62: Closer view of broken-lined square in Fig. 61 showing middle part of the shell section. Black arrow, the outer layer; white arrow, the middle layer; gray arrow, the inner layer; FIG. 63: Closer view of broken-lined square in Fig. 61 showing dorsal part of the shell section. Black arrow, the outer layer; white arrow, the middle layer; gray arrow, the inner layer; FIG. 64: Radial section of irregular fibrous prismatic structure of the outer layer; FIG. 65: Closer view of broken-lined square in Fig. 64. FIGS. 64, 65: Middle part of shell.



most part. The thickness of the nacre tablets is around  $0.8\ \mu\text{m}$  at the outer part, but thin inwards, reaching  $0.2\ \mu\text{m}$ .

*Myostracum*: Irregular blocky crystals to irregular simple prismatic structures (Figs. 76, 77).

Irregularly shaped acicular crystals that are approximately  $0.6\text{--}5\ \mu\text{m}$  in width and up to approximately  $20\ \mu\text{m}$  long in the long axes. At the thinned part, irregularly shaped blocky crystals that are up to approximately  $12\ \mu\text{m}$  in



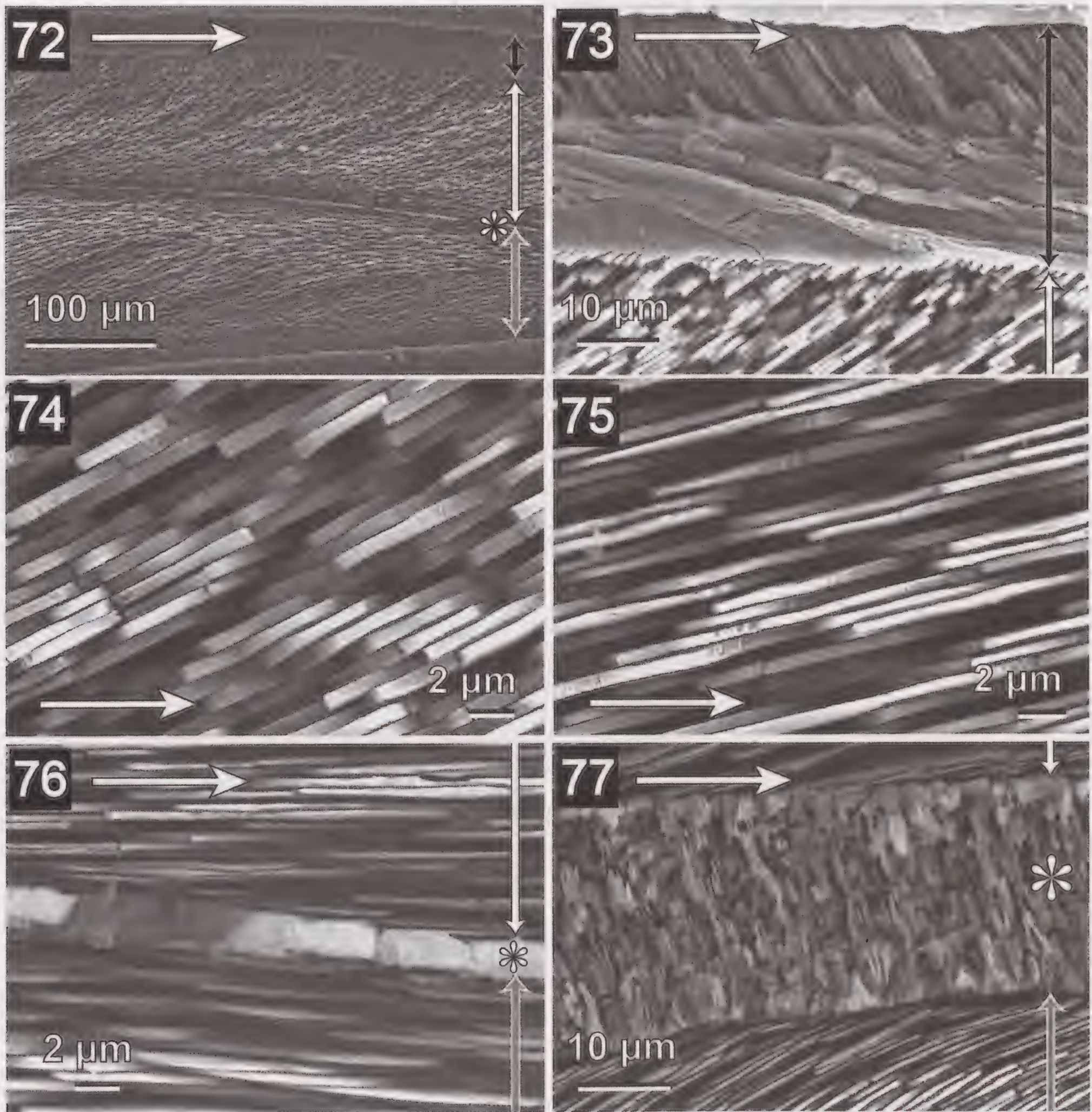
FIGS. 66–71. Scanning electron micrographs of *Acila insignis* microstructure. Growth direction is left in all images. FIG. 66: Radial section of columnar nacreous structure of the middle layer; FIG. 67: Closer view of broken-lined square in Fig. 66 showing columnar nacreous structure of the middle layer; FIG. 68: Nacreous structure of the middle and inner layers at middle part of shell. Myostracum consists of homogeneous structure. Vertical black arrow indicates the middle layer. Asterisk shows the myostracum and white arrow is the inner layer; FIG. 69: Radial section of nacreous structure of the middle and inner layers at dorsal part of shell. Myostracum is indistinct. Vertical black arrow indicates the middle layer and white arrow indicates the inner layer; FIG. 70: Radial section of sheet nacreous structure of the inner layer; FIG. 71: Closer view of broken-lined square in Fig. 70. FIGS. 66–68, 70, 71: Middle part of shell; FIG. 69: Dorsal part of shell.



width form the myostracum. This layer never becomes indistinct ventrally.

*Inner Layer.* Sheet nacreous (Figs. 75–77). Nacre tablets are approximately 0.5  $\mu\text{m}$  thick

and their width is around 3.5–18  $\mu\text{m}$ , piling-up like a brick wall. The nacre tablets in the inner layer are generally wider than those in the middle layer.



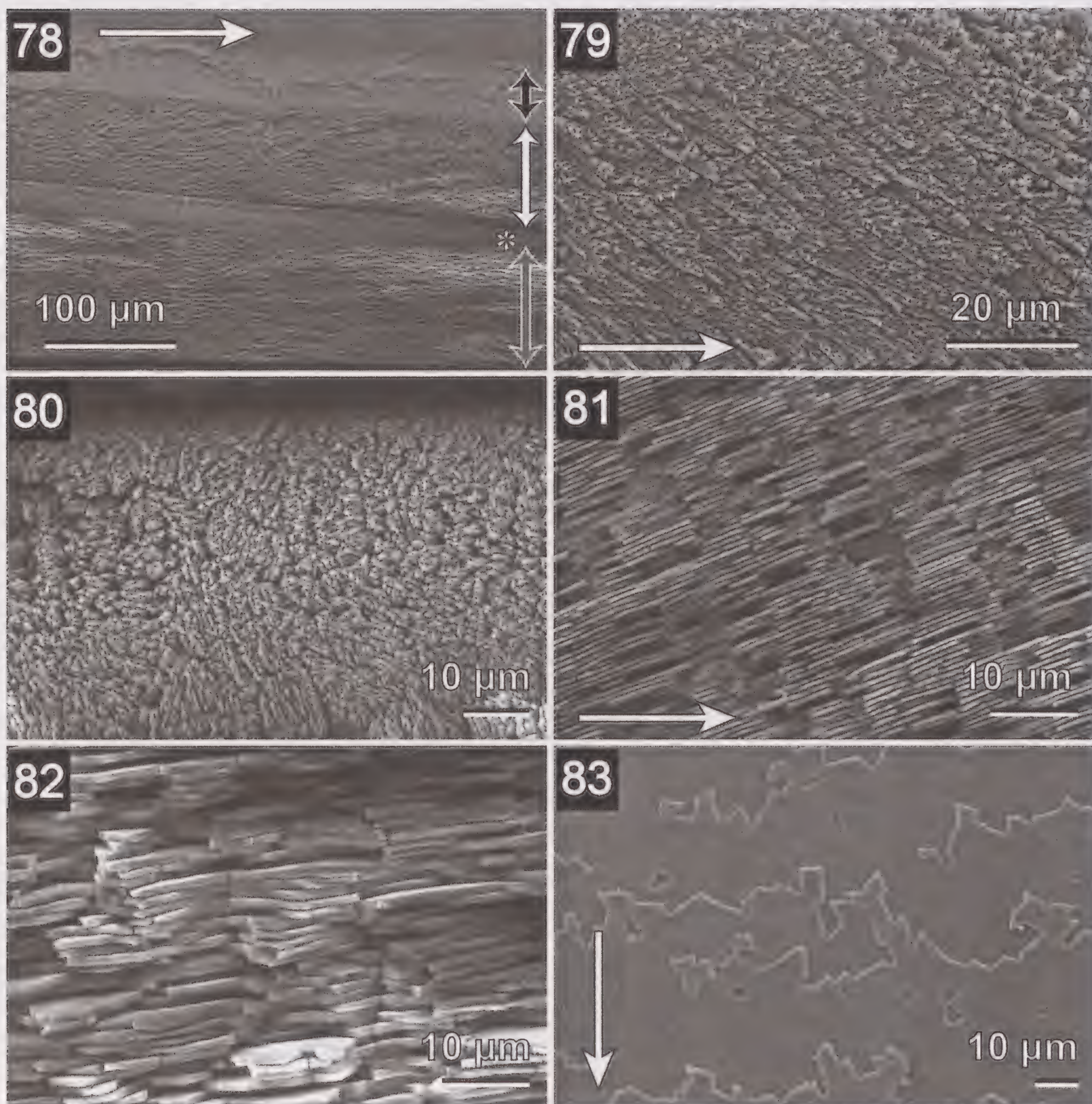
FIGS. 72–77. Scanning electron micrographs of *Brevinucula* sp. microstructure. Horizontal white arrow indicate growth direction. FIG. 72: Radial section. Black arrow, the outer layer; white arrow, the middle layer; asterisk, the myostracum; gray arrow, the inner layer; FIG. 73: Radial section of irregular fibrous prismatic structure type-A (Black arrow) and middle sheet nacreous layer (White arrow); FIG. 74: Radial section of sheet nacreous structure of the middle layer; FIG. 75: Radial section of sheet nacreous structure of the inner layer; FIG. 76: Radial section of nacreous structure of the middle and inner layers at ventral part of shell. Asterisk indicates myostracum. Vertical white arrow indicates the middle layer and gray arrow indicates the inner layer. Asterisk shows the myostracum; FIG. 77: Radial section of myostracum at dorsal part of shell. Asterisk indicates myostracum and vertical gray arrow indicates the middle layer. FIGS. 72–76: Middle part of shell; FIG. 77: Dorsal part of shell.



*Ennucula niponica* (Smith, 1885)  
(Figs. 5, 78–89)

**Shell Layers:** Outer, middle, myostracum, and inner layers are present (Fig. 78). The boundary between the innermost part of the outer layer and the outermost part of the middle

layer is smooth. The outer and middle layers thicken ventrally. The myostracum and inner layer generally thicken dorsally, whereas the thickest part is distributed in the middle part of a radial section. The shell is up to approximately 290  $\mu\text{m}$  thick in the observed specimen.



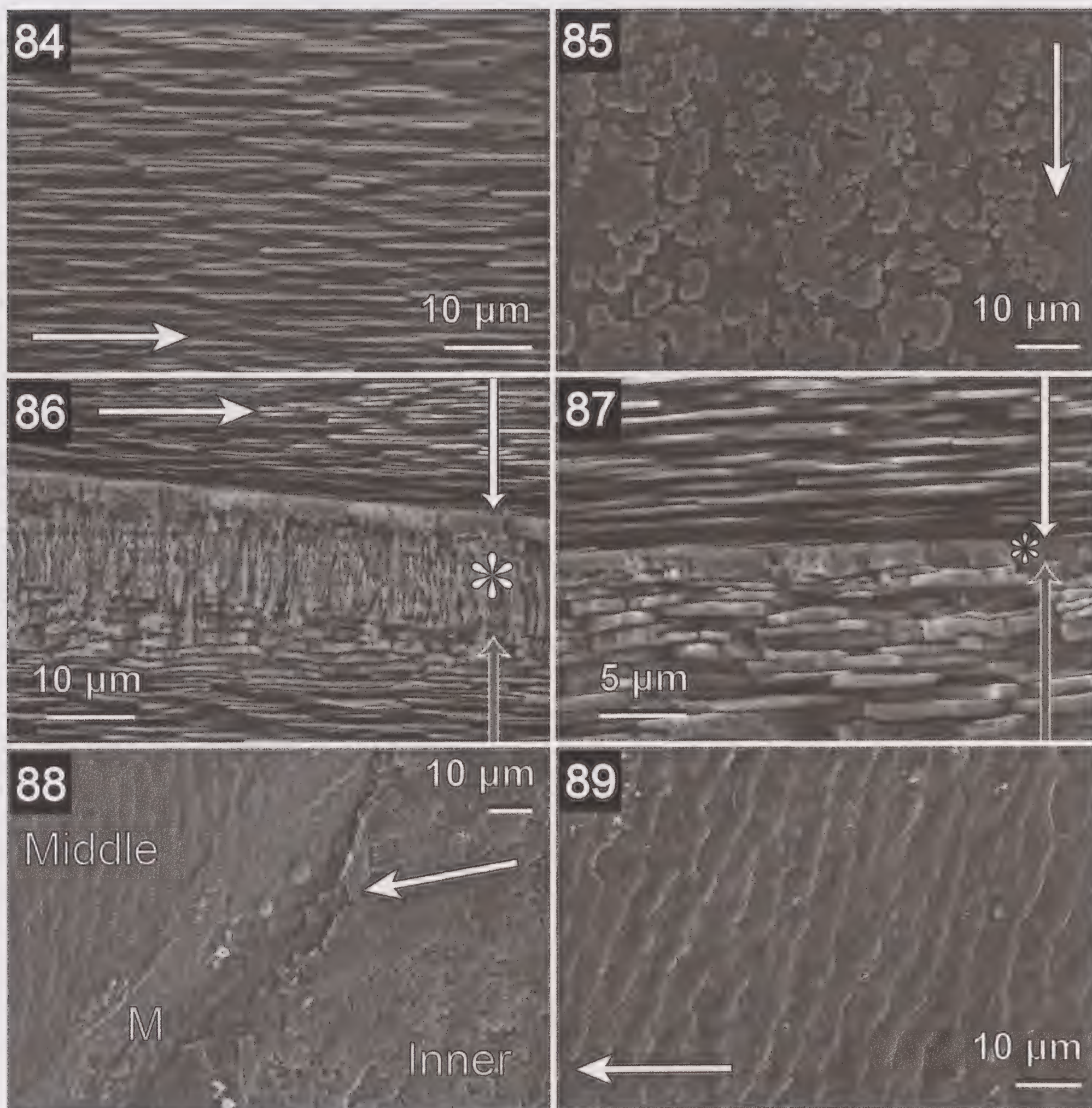
FIGS. 78–83. Scanning electron micrographs of *Ennucula niponica* microstructure. Horizontal white arrow indicate growth direction. FIG. 78: Radial section which comprised of the outer, middle, myostracum and inner layers. Black double-headed arrow, the outer layer; white double-headed arrow, the middle layer; asterisk, the myostracum; gray double-headed arrow, the inner layer; FIG. 79: Radial section of nondenticular composite prismatic structure of the outer layer; FIG. 80: Transverse section of nondenticular composite prismatic structure of the outer layer; FIG. 81: Radial section of columnar nacreous structure of the middle layer; FIG. 82: Transverse section of columnar nacreous structure of the middle layer; FIG. 83: Inner surface of columnar nacreous of the middle layer. FIG. 78: Dorsal part of shell; FIGS. 79–82: Middle part of shell; FIG. 83: Ventral part of shell.



**Outer Layer.** Nondenticular composite prismatic structure (NDCP, Figs. 78–80). The outer layer consists of acicular crystals (Figs. 79, 80). These crystals recline at angles of approximately 20–50° against the growth direction in the radial section and compose

the first-order prisms weakly radiating toward the depositional surface (Fig. 80).

**Middle Layer.** Columnar nacreous structure (Figs. 81–83). Nacre tablets are around 0.7  $\mu\text{m}$  thick at the outer part and have acute polygonal shapes (Fig. 83). Tablets stack



FIGS. 84–89. Scanning electron micrographs of *Ennucula niponica* microstructure. White arrow indicate growth direction. FIG. 84: Radial section of sheet nacreous structure of the inner layer; FIG. 85: Inner surface of sheet nacreous of the inner layer; FIG. 86: Radial section at dorsal part which comprised of the middle, myostracum and inner layers. Vertical white arrow, the middle layer; asterisk, the myostracum; gray arrow, the inner layer; FIG. 87: Radial section at middle part which comprised of the middle, myostracum and inner layers. Vertical white arrow, the middle layer; asterisk, myostracum; gray arrow, inner layer; FIG. 88: Inner surface around the posterior adductor muscle scar of left valve. Middle and myostracal layers distribute at the posterior adductor muscle scar. M, myostracum. FIG. 89: Closer view of the middle layer in Fig. 88. FIGS. 84, 85, 87: Middle part of shell; FIG. 86: Dorsal part of shell; FIGS. 88, 89: Ventral part of shell, around posterior adductor muscle scar.



vertically in the exterior side, while vertical stacking weakens inwards. At the innermost part of the middle layer, the thickness of the tablets reduces (up to 0.3  $\mu\text{m}$ ), and they become brick-like as in the inner layer that consists of sheet nacreous structures (Figs. 86, 87). Nacre columns stack on a tilt and are nearly vertical at the innermost part. While each tablet connects to the adjacent tablets in a narrow sense (Fig. 83), the width of each assumed independent tablets is around 7  $\mu\text{m}$ . Thickness of the tablets is approximately 1  $\mu\text{m}$  at the outer part of the middle layer and becomes thinner inwards, reaching 0.3  $\mu\text{m}$ . Nacre tablets are stepped as sheet nacreous structures (Fig. 83).

*Myostracum*: Irregular simple prismatic structure with irregular blocky crystals (Figs. 78, 86–88). The myostracum thickens dorsally and their thickness occupies the middle third of the total shell thickness. At the thickened part, the myostracum is composed of (1) the outer sublayer with irregular blocky crystals and irregular simple prismatic structure and (2) the inner sublayer with irregular acicular crystals around 0.8  $\mu\text{m}$  in the short axes (Fig. 86). At the thinned part, the layer is formed of irregular blocky crystals (Fig. 87). The myostracum definitely separates the middle and inner nacreous layers but their formation is not derived from the attached muscles. The middle layer is distributed at the adductor muscle scars, not the myostracum (Fig. 88).

*Inner Layer*: Sheet nacreous (Figs. 78, 84–89). Nacre tablets are approximately 0.7  $\mu\text{m}$  and brick-like (Fig. 84). The nacre tablets in the inner layer grow as rounded tablets, while those in the middle layer show acute polygonal shapes (Fig. 85). Independent nacre tablets are around 4–14  $\mu\text{m}$  in width and fused with adjacent tablets (Figs. 85, 88).

*Ennucula siberutensis*  
(Thiele & Jaeckel, 1931)  
(Figs. 6, 90–94)

*Shell Layers*: Outer, middle, myostracum, and inner layers are present (Figs. 90–94). The boundary between the innermost part of the outer layer and the outermost part of the middle layer is smooth. The boundary between the middle and inner layers is indistinct due to an obscure myostracum. The outer and middle layers thicken ventrally and the inner layer thickens dorsally. The shell is thickened in the ventral part and is approximately 360  $\mu\text{m}$  thick in the observed specimen.

*Outer Layer*: Irregular fibrous prismatic structure type-B (IFP type-B, new name, Figs. 91, 92). The IFP type-B in this species close to Irregular simple prismatic structure. The outer layer consists of acicular crystals whose width is relatively thick for fibrous prismatic structures (up to 4  $\mu\text{m}$ ), and the long axes curve in an obtuse L-shape in a radial section. Bended acicular prisms deeply recline at angles of approximately 80° against the growth direction in a radial section but at shallow angles of around 45° in the curved inwards portion.

*Middle Layer*: Sheet nacreous structure (Fig. 93). Nacre tablets are approximately 0.6  $\mu\text{m}$  thick brick-like and stack parallel to the long axes of acicular crystals of the inner sublayer of the outer layer and are nearly vertical at the innermost part.

*Myostracum*: This layer is obscure.

*Inner Layer*: Sheet nacreous (Fig. 94). Brick-like nacre tablets are approximately 0.4  $\mu\text{m}$  thick and their width is variable, up to 6  $\mu\text{m}$ .

*Ennucula tenuis* (Montagu, 1808)  
(Figs. 7, 95–103)

*Shell Layers*: Outer, middle, myostracum and inner layers are present (Figs. 95–97). The boundary between the innermost part of the outer layer and the outermost part of the middle layer is smooth. The outer and middle layers thicken ventrally. The myostracum and inner layer generally thicken dorsally, whereas the thickest part is distributed in the middle part of a radial section. The shell is up to approximately 240  $\mu\text{m}$  thick in the observed specimen.

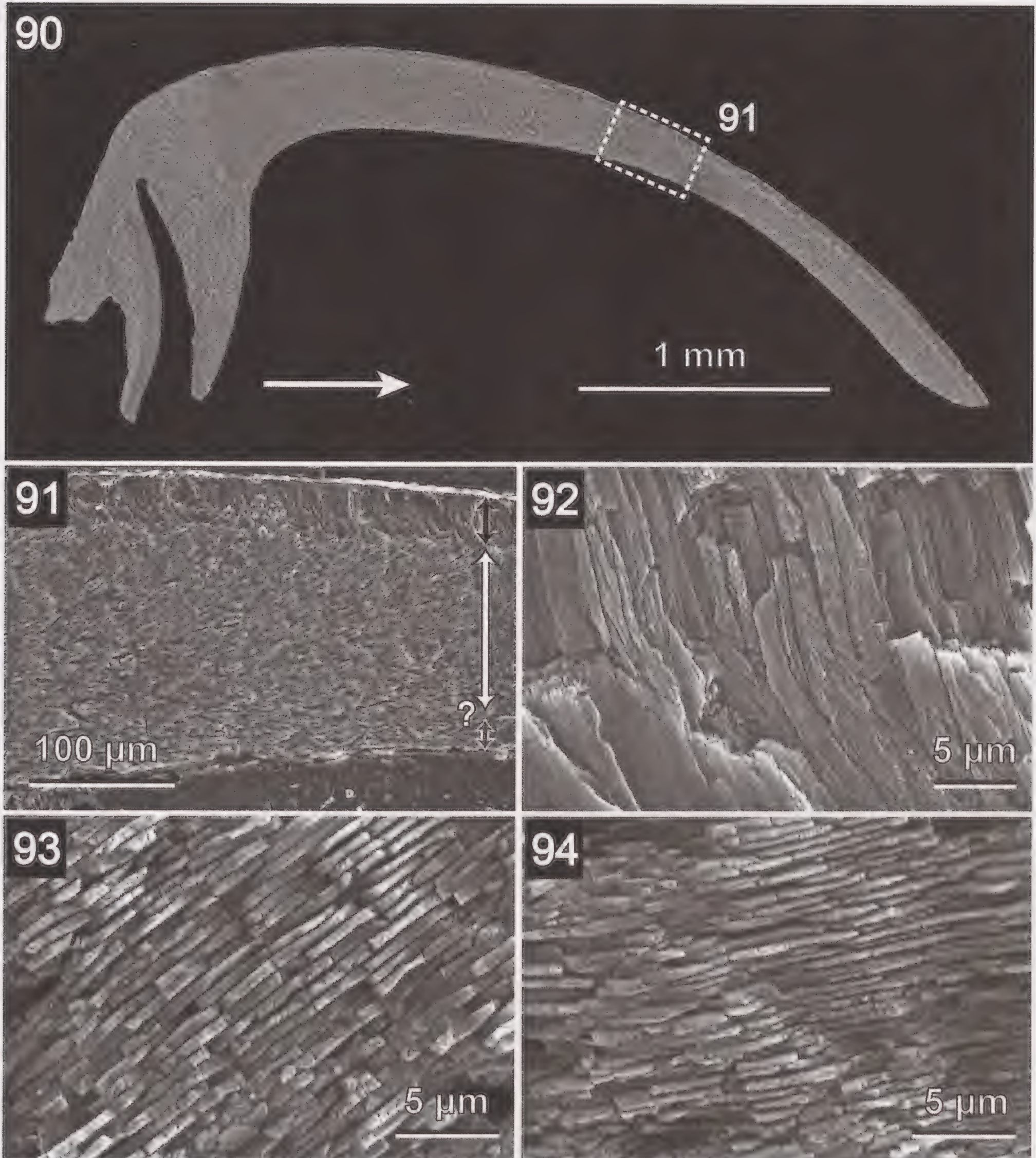
*Outer Layer*: Nondenticular composite prismatic structure (NDCP, Figs. 96–98). The outer layer consists of acicular crystals. These crystals recline at angles of around 60° against the growth direction in the radial section and compose the first-order prisms weakly radiating toward the depositional surface.

*Middle Layer*: Columnar nacreous to sheet nacreous structure (Figs. 99–102). Nacre tablets are around 0.7  $\mu\text{m}$  thick and stack vertically in the exterior side (Fig. 99), but gradually shift to irregularly stacked sheet nacre toward the shell interior (Fig. 101). At the innermost part of the middle layer, the thickness of the tablets reduces (up to 0.4  $\mu\text{m}$ ) and they become brick-like as in the inner layer, which consists of sheet nacre-



ous structures. While each tablet connects to the adjacent tablet in a narrow sense, the width of each assumed independent tablets is around 3–8  $\mu\text{m}$ .

*Myostracum*: Irregular simple prismatic structure (Figs. 101, 102). This structure consists of acicular and irregular shaped crystals.



FIGS. 90–94. Scanning electron micrographs of *Ennucula siberutensis* microstructure. Horizontal white arrow indicate growth direction. Growth direction is right side in Figs. 91–94. FIG. 90: Radial section of shell; FIG. 91: Closer view of broken-lined square in Fig. 90 showing middle part of the shell section. Black arrow, the outer layer; white arrow, the middle layer; gray arrow, the inner layer; FIG. 92: Radial section of irregular fibrous prismatic structure type-B of the outer layer; FIG. 93: Radial section of sheet nacreous structure of the middle layer; FIG. 94: Radial section of sheet nacreous structure of the inner layer. FIGS. 91–94: Middle part of shell.



**Inner Layer.** Sheet nacreous (Figs. 101–103). Nacre tablets are approximately  $0.6\ \mu\text{m}$  thick and brick-like. Independent nacre tablets are around  $3\text{--}12\ \mu\text{m}$  in width and fused with adjacent tablets.

*Ennucula* sp. 1  
(Figs. 8, 104–107)

**Shell Layers:** Outer, middle, myostracum, and inner layers are present (Figs. 104–107). The boundary between the innermost part of the outer layer and the outermost part of the middle layer is smooth. The myostracum is thin but separates the two layers (the middle and inner layer). The outer and middle layers thicken ventrally and the inner layer thickens dorsally. The shell is up to approximately  $280\ \mu\text{m}$  thick in the observed specimen.

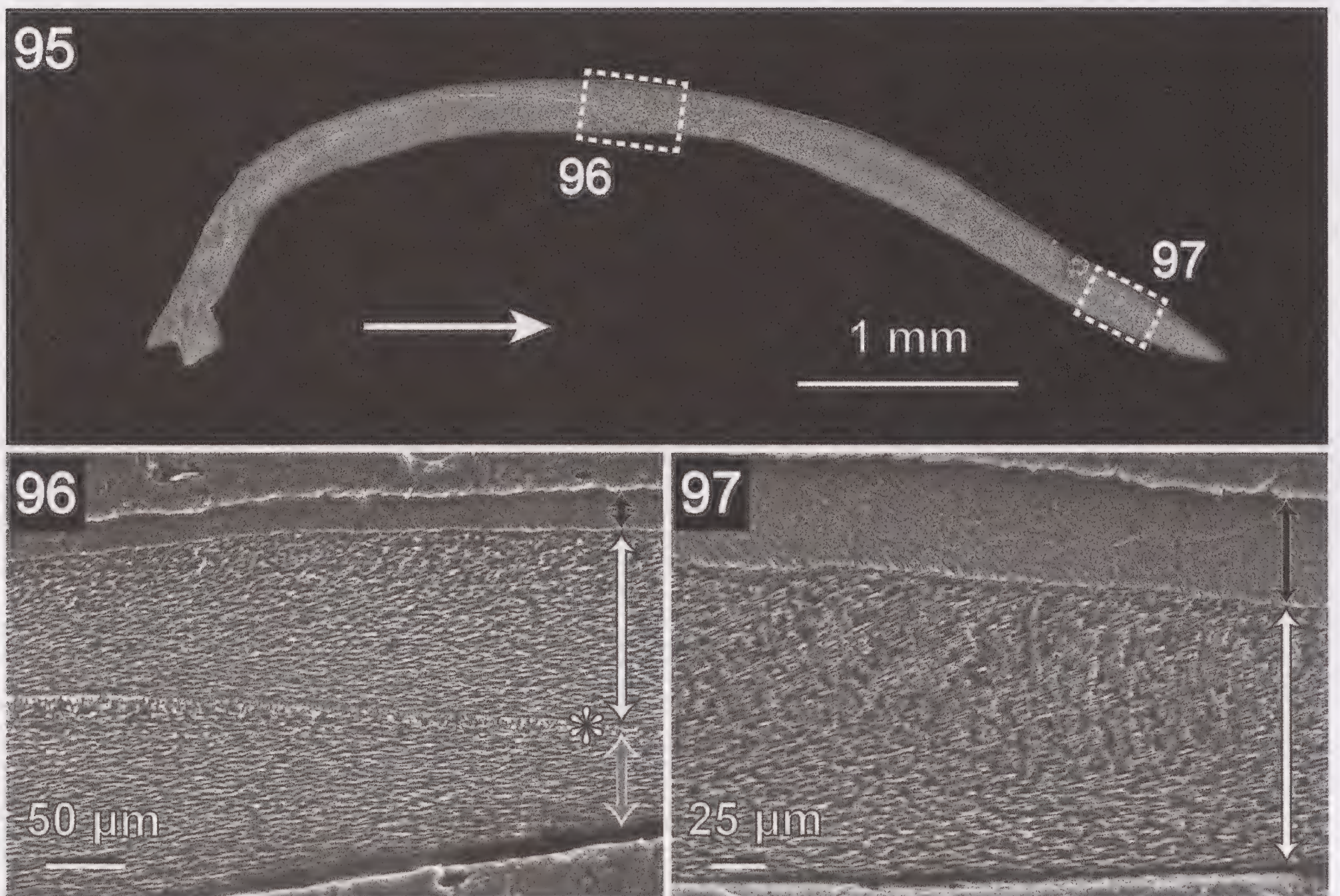
**Outer Layer.** Irregular fibrous prismatic structure type-B (IFP type-B, new name, Fig. 104). The outer layer consists of acicular crystals whose width is relatively thick for fibrous prismatic (up to  $10\ \mu\text{m}$ ) and the long

axes curves, showing an obtuse L-shape in a radial section. Bended acicular prisms recline at an angle of approximately  $70^\circ$  against the growth direction in a radial section but at shallow angles of around  $20^\circ$  after being curved inwards.

**Middle Layer.** Columnar to sheet nacreous structure (Figs. 105, 106). Tablets weakly stack vertically in the exterior side, while vertical stacking weakens inwards. Nacre tablets are around  $0.7\ \mu\text{m}$  thick,  $1.7\text{--}9\ \mu\text{m}$  in width and become thinner inwards (up to  $0.4\ \mu\text{m}$ ). Tablets stack on a tilt parallel to the long axes of acicular crystals of the outer layer at the outermost part of the middle layer and nearly vertically at the innermost part of it.

**Myostracum:** Homogeneous structure (Fig. 106). The myostracum layer is very thin (less than  $0.4\ \mu\text{m}$ ) and consists of granular crystals that are around  $0.7\ \mu\text{m}$  in diameter.

**Inner Layer.** Sheet nacreous (Figs. 106, 107). Nacre tablets which pile up like a brick wall are approximately  $0.2\ \mu\text{m}$  thick and their width is variable (up to  $12\ \mu\text{m}$ ).



FIGS. 95–97. Scanning electron micrographs of *Ennucula tenuis* microstructure. Horizontal white arrow indicate growth direction. FIG. 95: Radial section of shell; FIG. 96: Closer view of broken-lined square in Fig. 95 showing middle part of the shell section. Black arrow, the outer layer; white arrow, the middle layer; asterisk, the myostracum; gray arrow, the inner layer. FIG. 97: Closer view of broken-lined square in Fig. 95 showing ventral part of the shell section. Black arrow, the outer layer; white arrow, the middle layer.

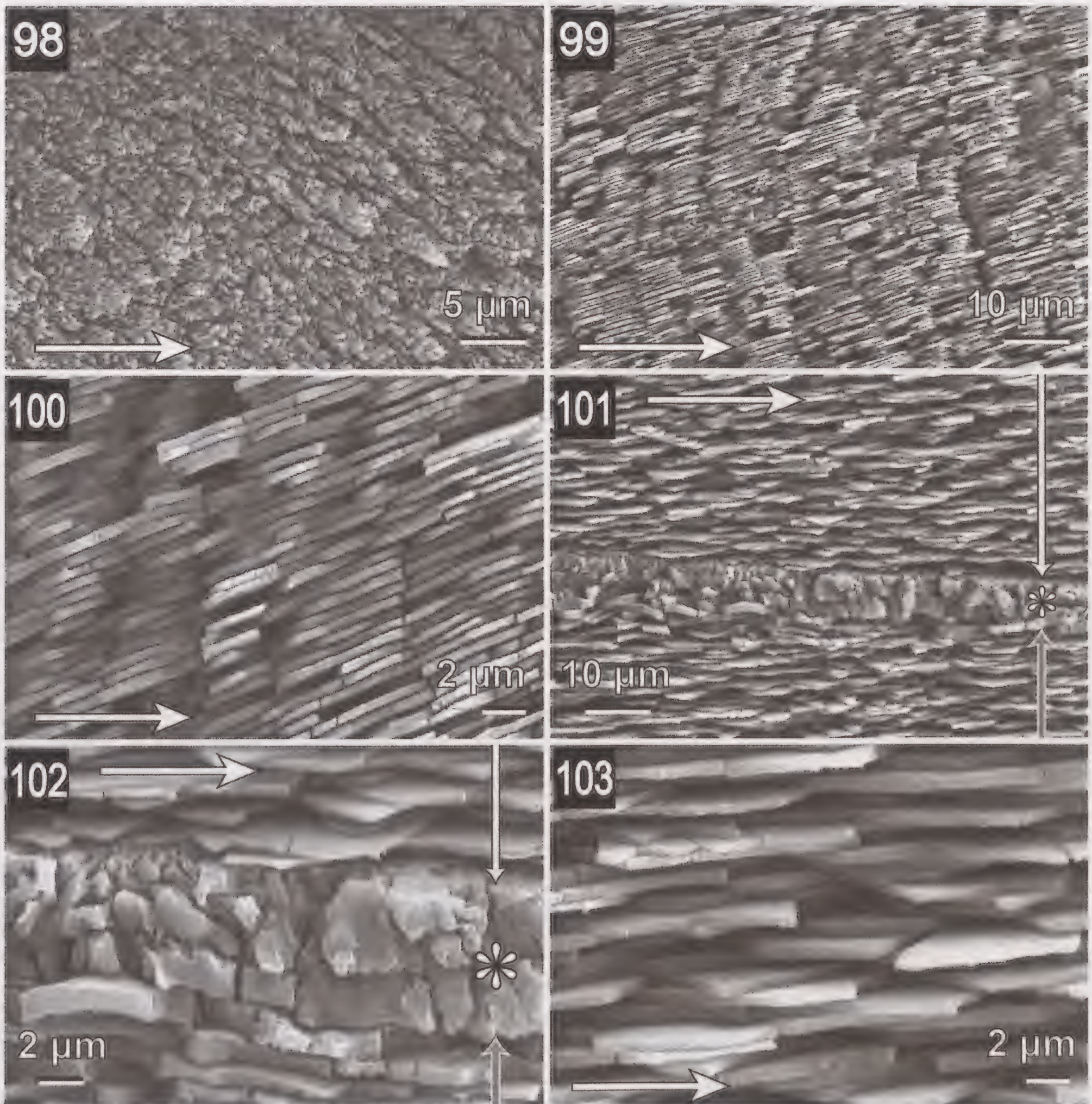


*Ennucula* sp. 2  
(Figs. 9, 108–111)

**Shell Layers:** Outer, middle, myostracum and inner layers are present (Figs. 108–111). The boundary between the two layers is indistinct due to an obscure myostracum. The outer and middle layers thicken ventrally. The inner

layer lies dorsal to the pallial line and generally thickens dorsally whereas its thickest part is distributed in the middle part of a radial section. The shell is up to approximately 360  $\mu\text{m}$  thick in the observed specimen.

**Outer Layer:** Irregular spherulitic prismatic structure (ISphP; Fig. 108). Acicular crystals are arranged parallel to one another tilting at an



FIGS. 98–103. Scanning electron micrographs of *Ennucula tenuis* microstructure. Horizontal white arrow indicate growth direction. FIG. 98: Radial section of nondenticular composite prismatic structure of the outer layer; FIG. 99: Radial section of columnar nacreous structure of the middle layer; FIG. 100 Closer view of columnar nacreous structure of the middle layer; FIG. 101: Radial section at middle part which comprised of the middle, myostracum and inner layers. Vertical white arrow, the middle layer; asterisk, the myostracum; gray arrow, the inner layer; FIG. 102: Closer view of Fig. 101. Vertical white arrow, the middle layer; asterisk, the myostracum; white arrow, the inner layer; FIG. 103: Radial section of sheet nacreous structure of the inner layer. FIGS. 98–100: Ventral part of shell; FIGS. 102, 103: Middle part of shell.



angle of around  $55^\circ$  against the growth direction in a radial section. These crystals thicken inwards by approximately 0.4 to 2  $\mu\text{m}$ .

**Middle Layer:** Columnar nacreous to sheet nacreous structures (Figs. 109, 110). Nearly polygonal tablets stack vertically in the exterior side (Fig. 109), while vertical stacking weakens inwards. At the innermost part of the middle layer, they pile up like a brick wall, similar to the sheet nacreous structure in the inner layer (Fig. 110). Nacre columns stack on a tilt parallel to the long axes of the acicular crystals of the outer layer at the outermost part of the middle layer and nearly vertically at its innermost part. The width of the independent tablets is around 7–13  $\mu\text{m}$  at the outer part. The thickness of the tablets is approximately 1  $\mu\text{m}$  at the outer part of the middle layer, thinning inwards and reaching 0.5  $\mu\text{m}$ .

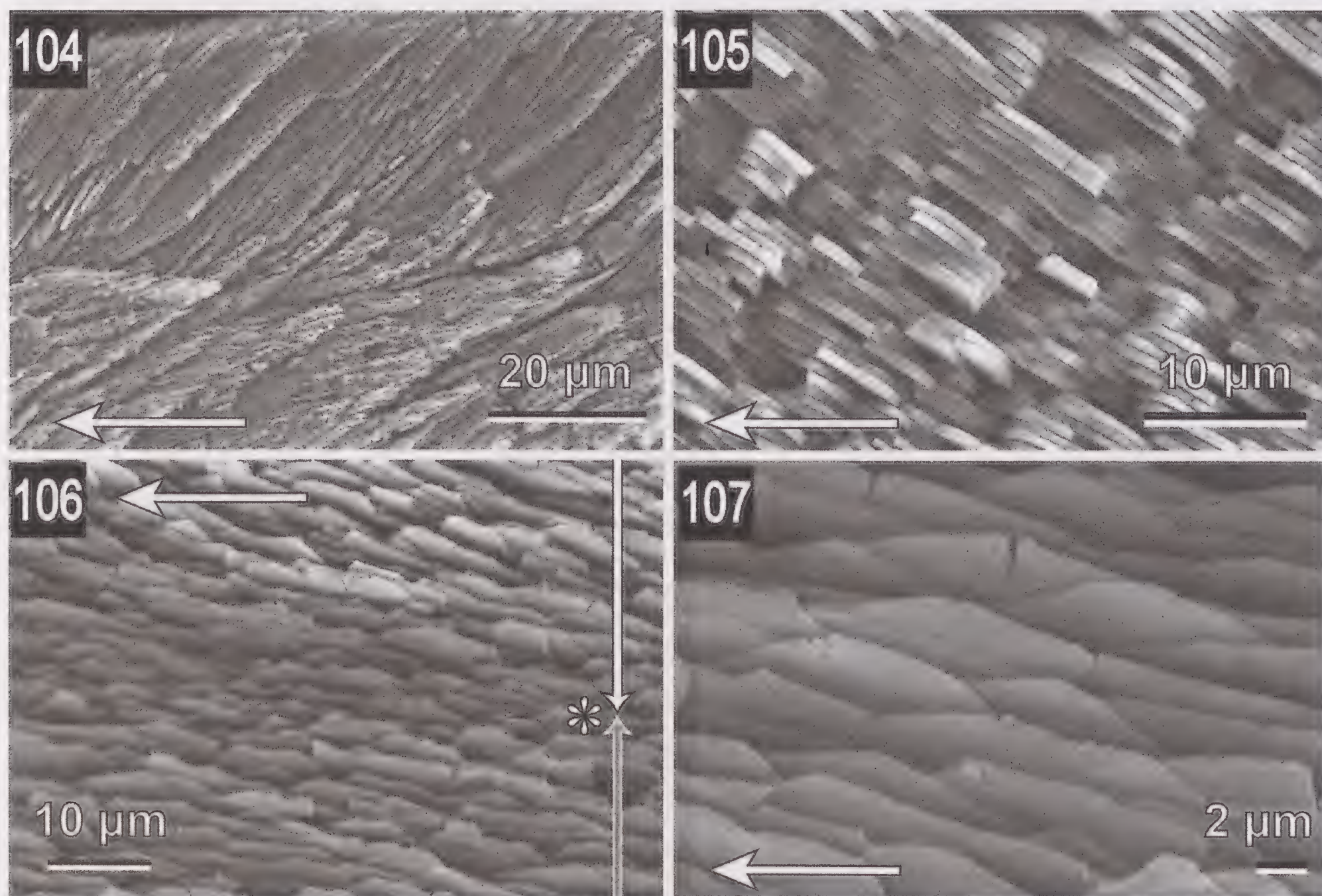
**Myostracum:** The myostracum of this species is obscure and is probably a homogeneous structure.

**Inner Layer:** Sheet nacreous (Fig. 111). Nacre tablets that are approximately 0.6  $\mu\text{m}$  thick pile up like brick wall. Their width is around 3–10  $\mu\text{m}$ .

*Nucula* sp.  
(Figs. 10, 112–117)

**Shell Layers:** Outer, middle, myostracum and inner layers are present (Figs. 112–117). The outer and middle layers thicken ventrally and the myostracum and inner layer thicken dorsally. The shell is up to approximately 235  $\mu\text{m}$  thick in the observed specimen.

**Outer Layer:** Denticular composite prismatic structure (Figs. 112–114). Acicular crystals spread like a fan ventrally (Fig. 114) because these crystals are oriented perpendicular to the deposit surface (note correspondence between growth lines and the orientation of acicular crystals in Fig. 112). In a transverse section, the boundary between the innermost



FIGS. 104–107. Scanning electron micrographs of *Ennucula* sp. 1 microstructure. Horizontal white arrow indicate growth direction. FIG. 104: Radial section of irregular fibrous prismatic structure type-B of the outer layer; FIG. 105: Radial section of sheet nacreous structure of the middle layer; FIG. 106: Radial section of nacreous structure of the middle and inner layers. Myostracum is obscure. Vertical white arrow indicates the middle layer and gray arrow indicates the inner layer; FIG. 107: Radial section of sheet nacreous structure of the inner layer. FIGS. 104–107: Middle part of shell.



part of the outer layer and the outermost part of the middle layer is recognized as a dentate line due to a crenulate internal ventral margin. The width of crystals is around 3  $\mu\text{m}$ .

**Middle Layer.** Sheet nacreous structure (Figs. 115, 116). Nearly polygonal tablets that are approximately 0.7  $\mu\text{m}$  thick pile up like a brick wall (Fig. 115). Nacre columns stack on a tilt parallel to the long axes of the acicular crystals of the outer layer at the outermost part of the middle layer and nearly vertically at its innermost. The boundary of adjacent tablets is indistinct but their width is around 4–14  $\mu\text{m}$ .

**Myostracum:** Irregular simple prismatic structure (Fig. 116). Irregular shaped acicular crystals compose this layer. The myostracum layer thickens dorsally.

**Inner Layer.** Sheet nacreous (Figs. 116, 117). Nacre tablets are approximately 0.7  $\mu\text{m}$  thick and pile up like bricks almost parallel to the

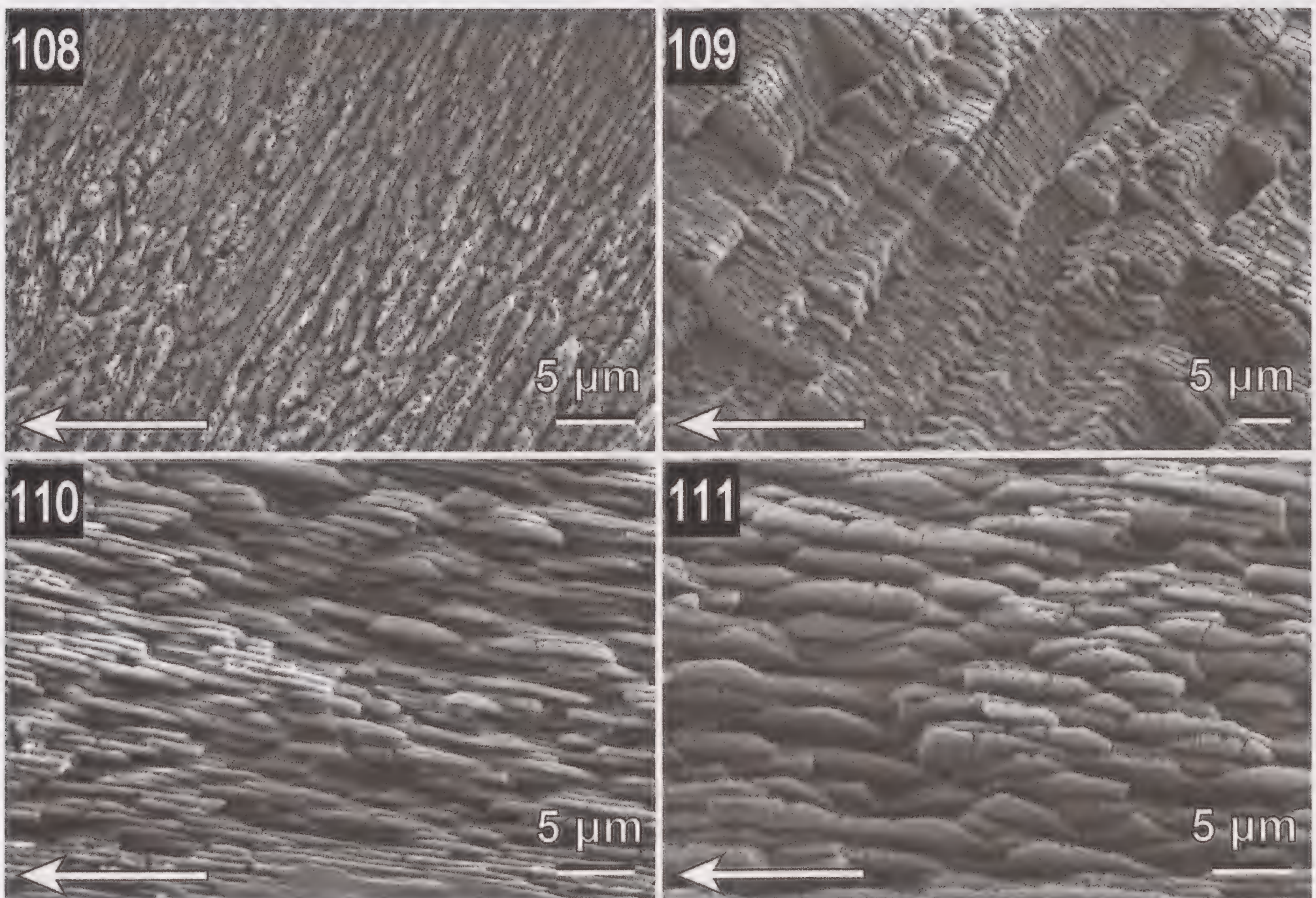
inner shell surface. Although the boundary of adjacent tablets is indistinct, their width is variable (around 4–20  $\mu\text{m}$ ).

*Nucula gemmulata* Habe, 1953  
(Figs. 11, 118–123)

**Shell Layers:** Outer, middle, myostracum and inner layers are present (Figs. 118–123). The outer and middle layers thicken ventrally, and the myostracum and inner layer thicken dorsally. The shell thickness is up to approximately 480  $\mu\text{m}$  thick in the observed specimen.

**Outer Layer.** Denticular composite prismatic structure (Figs. 118–120). Acicular crystals spread ventrally like a fan perpendicularly to the deposit surface. The width of the crystals is around 1  $\mu\text{m}$ .

**Middle Layer:** Sheet nacreous structure; barely columnar nacreous structure (Figs.

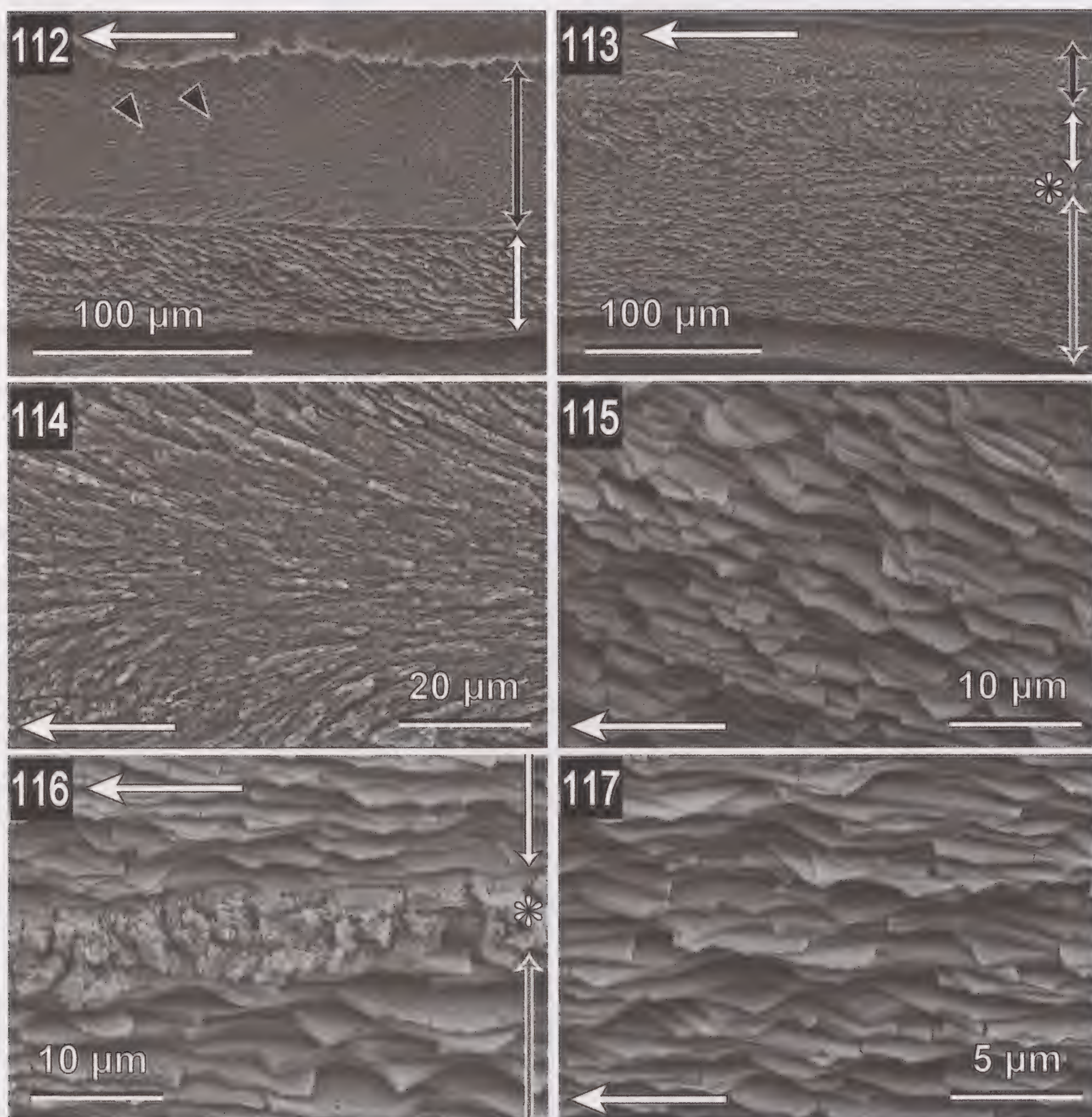


FIGS. 108–111. Scanning electron micrographs of *Ennucula* sp. 2 microstructure. White arrow indicate growth direction. FIG. 108: Radial section of irregular spherulitic prismatic structure of the outer layer; FIG. 109: Radial section of columnar nacreous structure of outer part in the middle layer; FIG. 110: Radial section of sheet nacreous structure of inner part in the middle layer; FIG. 111: Radial section of sheet nacreous structure of the inner layer. FIGS. 108–110: Ventral part of shell; FIG. 111: Dorsal part of shell.



121, 122). Sheet nacreous structure is dominant in this layer, and tablets are slightly vertically stacked. Nearly polygonal tablets are around  $0.6\ \mu\text{m}$  thick at the outer part and

thinner inwards (around  $2\ \mu\text{m}$ ). Nacre columns stack on a tilt parallel to the long axes of the acicular crystals of the outer layer at the outermost part of the middle layer and

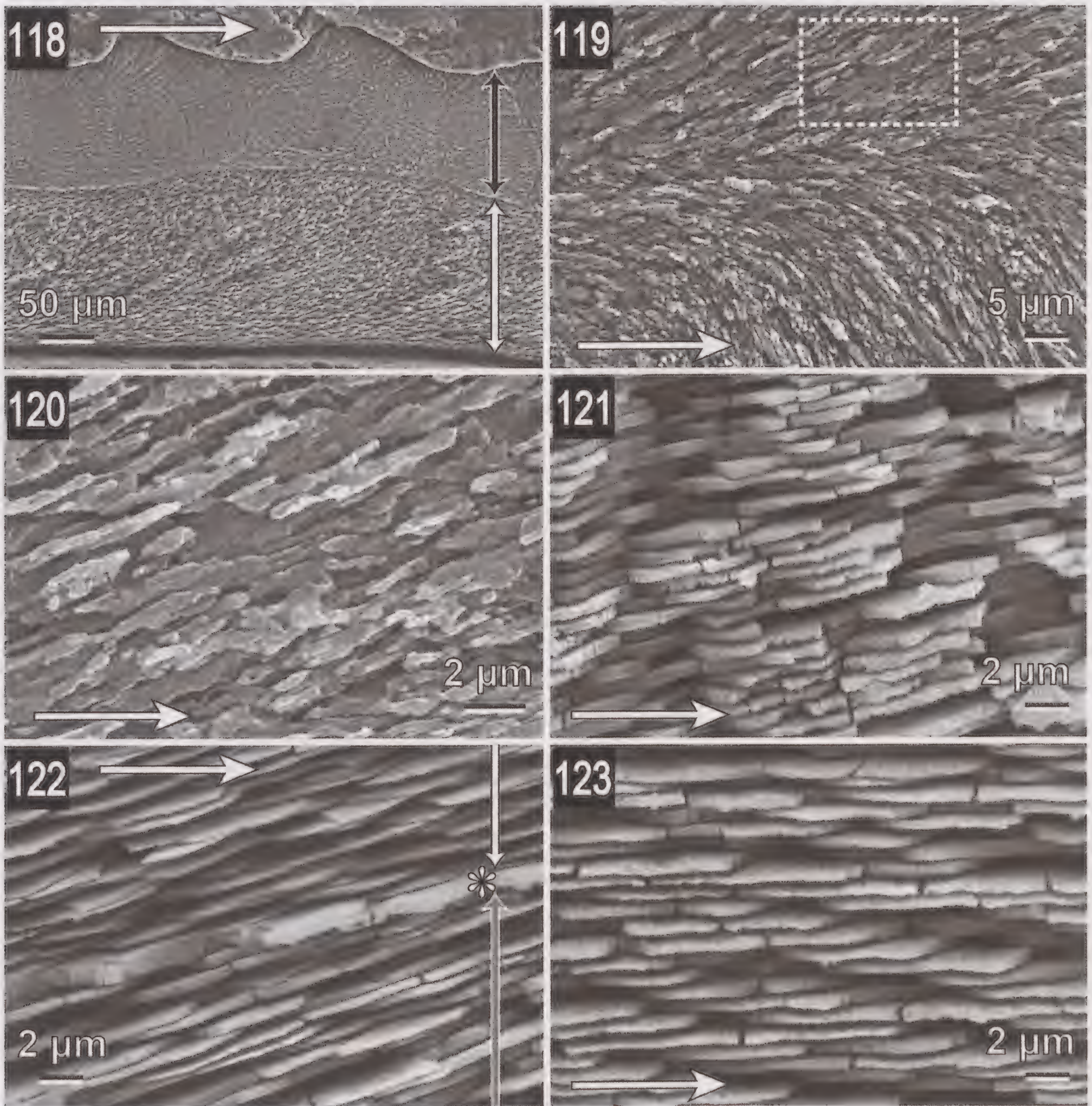


FIGS. 112–117. Scanning electron micrographs of *Nucula* sp. microstructure. White arrow indicate growth direction. FIG. 112: Radial section at ventral part of shell which comprised of the outer and middle layers. Black double-headed arrow, the outer layer; white double-headed arrow, the middle layer. Black arrow-heads indicate growth lines; FIG. 113: Radial section at dorsal part of shell which comprised of the outer, middle, myostracum and inner layers. Black double-headed arrow, the outer layer; white double-headed arrow, the middle layer; asterisk, the myostracum; gray double-headed arrow, the inner layer; FIG. 114: Radial section of denticular composite prismatic structure of the outer layer; FIG. 115: Radial section of sheet nacreous structure of the middle layer; FIG. 116: Radial section which comprised of the middle, myostracum and inner layers. Vertical black arrow, the middle layer; asterisk, the myostracum; white arrow, the inner layer; FIG. 117: Radial section of sheet nacreous structure of the inner layer. FIGS. 112, 114, 115: Ventral part of shell; FIGS. 113, 116, 117: Dorsal part of shell.



nearly vertically at the innermost part. The boundary of adjacent tablets is indistinct but their width is around 2.5–5  $\mu\text{m}$  at the outer part and 3–18  $\mu\text{m}$  at the inner part.

*Myostracum*: Irregular blocky crystals (Fig. 122). At the ventral side of the shell where this layer is mostly thickened, irregularly shaped blocky crystals, like a sort of false



FIGS. 118–123. Scanning electron micrographs of *Nucula gemmulata* microstructure. White arrow indicate growth direction. FIG. 118: Radial section at ventral part of shell which comprised of the outer and middle layers. Black double-headed arrow, the outer layer; white double-headed arrow, the middle layer; FIG. 119: Radial section of denticular composite prismatic structure of the outer layer; FIG. 120: Closer view of broken-lined square in Fig. 119; FIG. 121: Radial section of probable columnar nacreous structure of the middle layer; FIG. 122: Radial section which comprised of the middle, myostracum and inner layers. Vertical black arrow, the middle layer; asterisk, the myostracum; white arrow, the inner layer; FIG. 123: Radial section of sheet nacreous structure of the inner layer. FIGS. 118, 121: Ventral part of shell; FIGS. 119, 120, 123: Middle part of shell; FIG. 122: Dorsal part of shell.

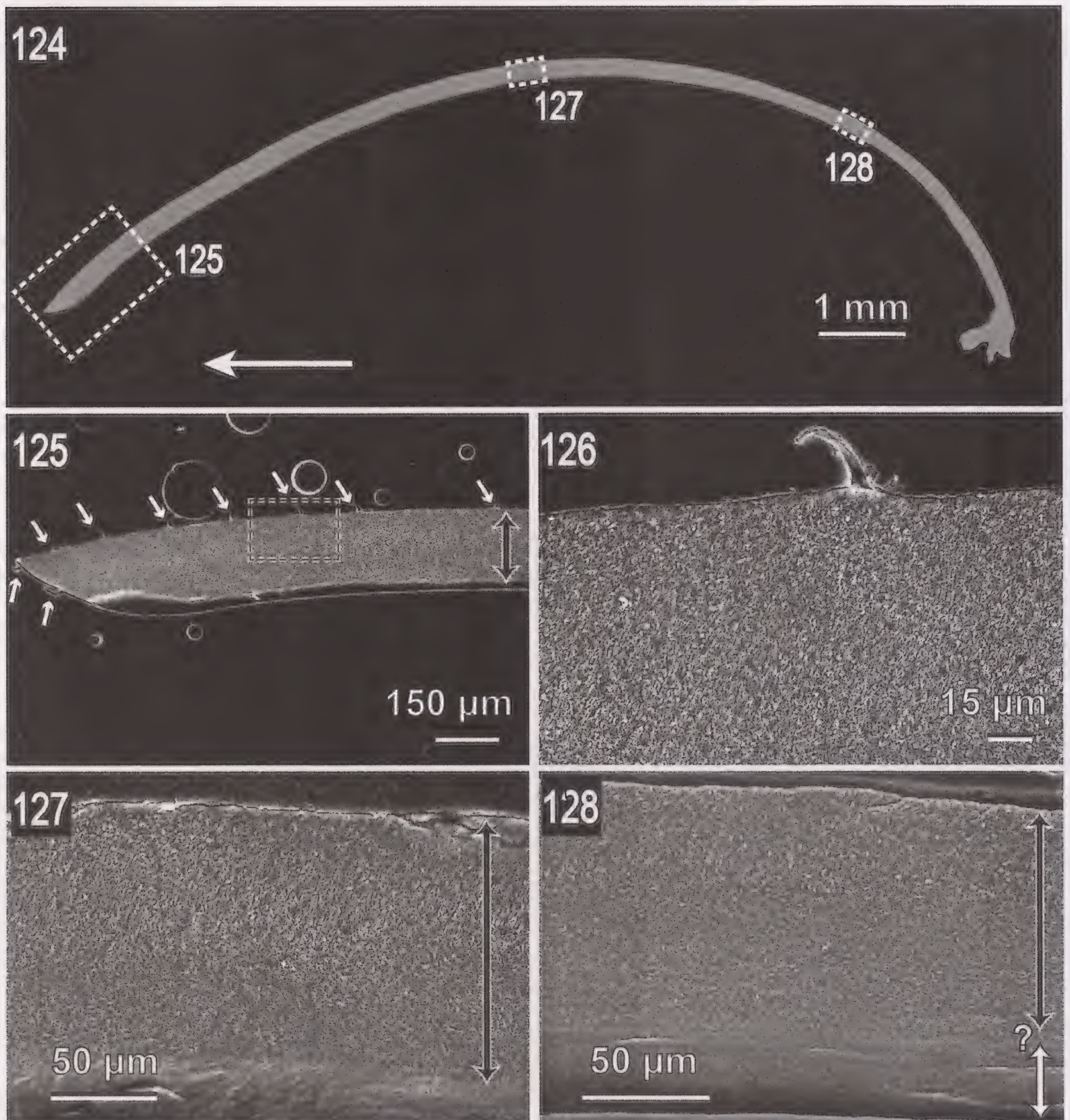


nacre tablets, compose the myostracum and become obscure ventrally.

*Inner Layer.* Sheet nacreous (Figs. 122, 123).

Nacre tablets are approximately 0.2–0.4

$\mu\text{m}$  thick, and almost parallel to the inner shell surface. Their width is variable (around 4–10  $\mu\text{m}$ ).



FIGS. 124–128. Scanning electron micrographs of *Sarepta speciosa* microstructure. White arrow indicate growth direction. FIG. 124: Radial section of shell; FIG. 125: Closer view of broken-lined square in Fig. 124 showing ventral part of the shell section. Black double-headed arrow, the outer layer; white arrow, commarginal rib of periostracum; FIG. 126: Closer view of broken-lined square in Fig. 125; FIG. 127: Closer view of broken-lined square in Fig. 124 showing middle part of the shell section. Black double-headed arrow, the outer layer; FIG. 128: Closer view of broken-lined square in Fig. 124 showing dorsal part of the shell section. Black double-headed arrow, the outer layer; White double-headed arrow, the inner layer; Question mark implies obscure margin of two layers.



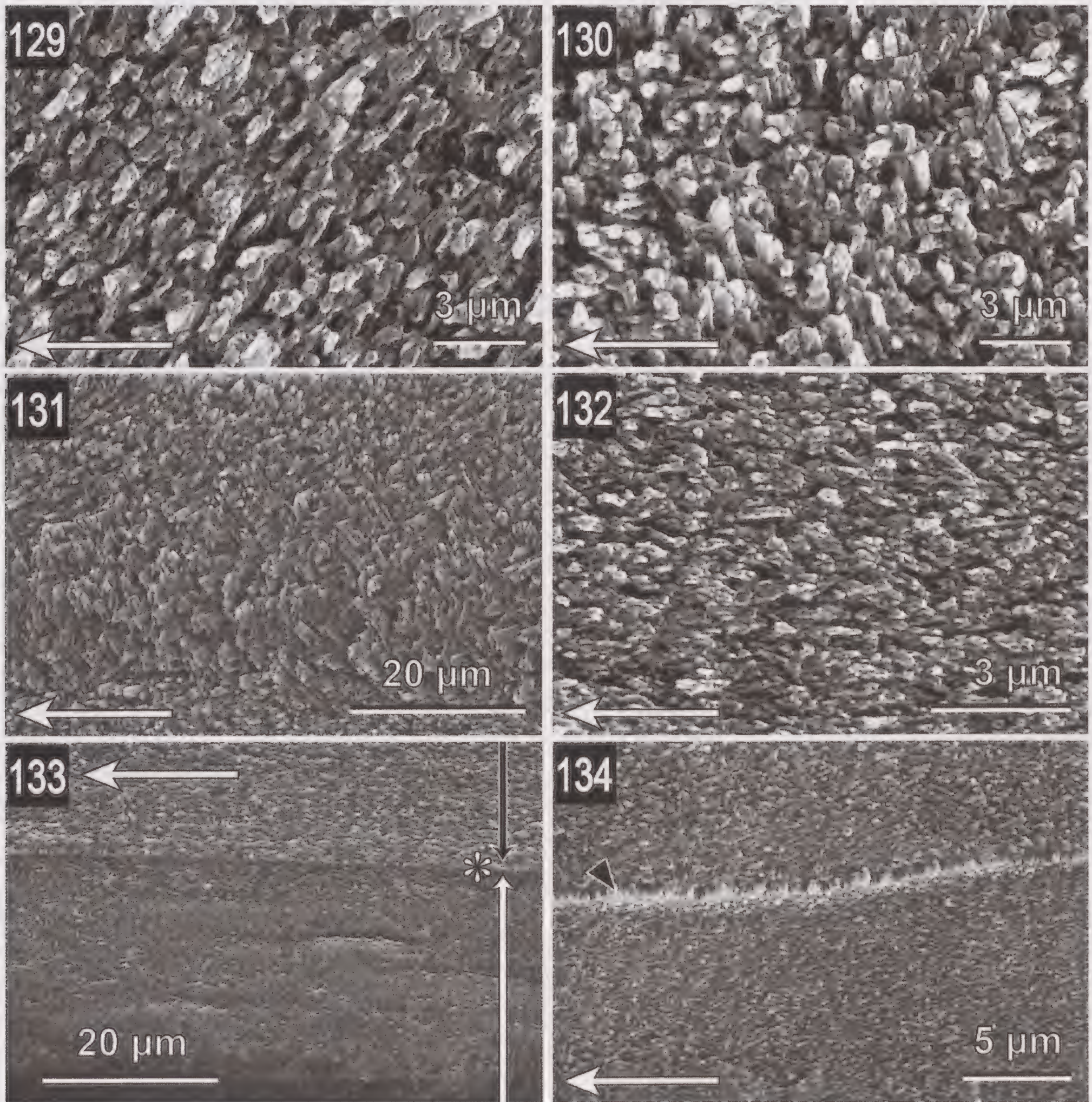
## Family Sareptidae

*Sarepta speciosa* A. Adams, 1860  
(Figs. 12, 124–134)

*Shell Layers:* Outer, myostracum and inner layers are present. The outer layer weakly thickens ventrally, and the shell thickens

up to 213  $\mu\text{m}$ . The inner layer shows poor growth. The inner layer is restricted to the dorsal part, and it is questionable whether the myostracum reaches the pallial line.

*Outer Layer:* Mostly homogeneous structure (Figs. 124–130, 132–134). A fine complex crossed lamellar structure is barely



FIGS. 129–134. Scanning electron micrographs of *Sarepta speciosa* microstructure. White arrows indicate growth direction. FIG. 129: Radial section of homogeneous structure of outer part of the outer layer; FIG. 130: Radial section of homogeneous structure of middle part of the outer layer; FIG. 131: Radial section of fine complex crossed lamellar structure of outer part at dorsal part of shell; FIG. 132: Radial section of homogeneous structure of inner part of the outer layer; FIG. 133: Radial section which comprised of the outer, myostracum and inner layers. Vertical black arrow, the outer layer; asterisk, the myostracum; white arrow, the inner layer; FIG. 134: Radial section of homogeneous structure of the inner layer. Black arrow-head indicates the growth line. FIGS. 129–132: Middle part of shell; FIGS. 133, 134: Dorsal part of shell.



recognized (Fig. 131). Granular crystals composed of a homogeneous structure moderately diminish in diameter inwards. The average diameter of the granular crystals is around 1.2  $\mu\text{m}$  at the outer part (Fig. 129) and 0.4  $\mu\text{m}$  at the inner part (Fig. 132). A fine complex crossed lamellar structure is recognized at the middle part of the outer layer in the dorsal and ventral sides along the growth lines (Fig. 131). Acicular crystals composed of first-order lamellae of fine complex crossed lamellar structure are up to 6  $\mu\text{m}$  long in the long axes and incline at around  $15^\circ$  to the deposit surface and growth line.

*Myostracum*: Irregular simple prismatic structure (Figs. 133, 134). Very thin (up to 0.8  $\mu\text{m}$ ) and generally obscure. Acicular crystals composing the myostracum are around 0.4  $\mu\text{m}$  at the thickest part.

*Inner Layer*: Homogeneous structure (Figs. 133, 134). Granular crystals of homogeneous structure are far smaller than those in the middle layer (around 0.2  $\mu\text{m}$  in diameter).

*Setigloma japonica* (Smith, 1885)  
(Figs. 13, 135–140)

*Shell Layers*: Outer, myostracum and inner layers are present (Fig. 135). The outer and inner layers thicken ventrally, whereas the thickest part is in the middle of a radial section. The shell is up to approximately 120  $\mu\text{m}$  thick in the observed specimen.

*Outer Layer*: Fine complex crossed lamellar structure (Figs. 135–139). Acicular crystals composing first-order lamellae of fine complex crossed lamellar structure are around 0.3  $\mu\text{m}$  wide, up to 5  $\mu\text{m}$  along the long axes, and inclined at around  $15^\circ$  to the deposit surface (i.e. growth line). Acicular crystals in the innermost part are larger than those in the outermost part. Irregular simple prismatic structure comprised of aligned acicular crystals is recognized at the growth lines (Fig. 138). Acicular crystals are 0.5  $\mu\text{m}$  in width.

*Myostracum*: Irregular simple prismatic structure (Figs. 135, 139). The average width of these crystals is 0.5  $\mu\text{m}$ .

*Inner Layer*: Fine complex crossed lamellar structure (Figs. 135, 139, 140). Acicular crystals composing first-order lamellae are around 0.3  $\mu\text{m}$  wide and up to 5  $\mu\text{m}$  long in the long axes and inclined at around  $15^\circ$  to

the deposit surface. Several growth lines are recognized in the irregular simple prismatic structure (Fig. 135).

Superfamily Manzanelloidea  
Family Nucinellidae  
*Huxleyia sulcata* Adams, 1860  
(Figs. 14, 141–145)

*Shell Layers*: No layer construction is recognized due to the obscure or absent myostracum (Figs. 141, 142). Thick periostracum with 10  $\mu\text{m}$  average thickness covers the outer surface of the shell, periodically thickens inwards, and intrudes into the shell, where dark colored concentric ribs are recognized at the exterior shell surface (Fig. 142). The shell thickens ventrally, reaching 142  $\mu\text{m}$ .

*Shell Microstructures*: Mostly homogeneous structure and partly fine complex crossed lamellar structure (Fig. 142, 144). The homogeneous structure is composed of granular crystals that are around 1  $\mu\text{m}$  thick. Second-order crystals are less than 150 nm in diameter (Fig. 144). A fine complex crossed lamellar structure is distributed at the top one-third part of the shell. Acicular crystals in the fine complex crossed lamellar structure are 1  $\mu\text{m}$  wide, up to 7  $\mu\text{m}$  long in the long axes, and inclined at around  $20^\circ$  to the shell surface. At the inner part of the shell, several growth lines are distributed nearly parallel to the inner shell surface. Irregular simple prismatic structure composed of acicular crystals (up to 3  $\mu\text{m}$  long, around 1  $\mu\text{m}$  width) was observed at growth lines (Figs. 143, 145). No growth lines are developed at the outer part of the shell, even where the periostracum thickens inwards, where growth breaks might have occurred.

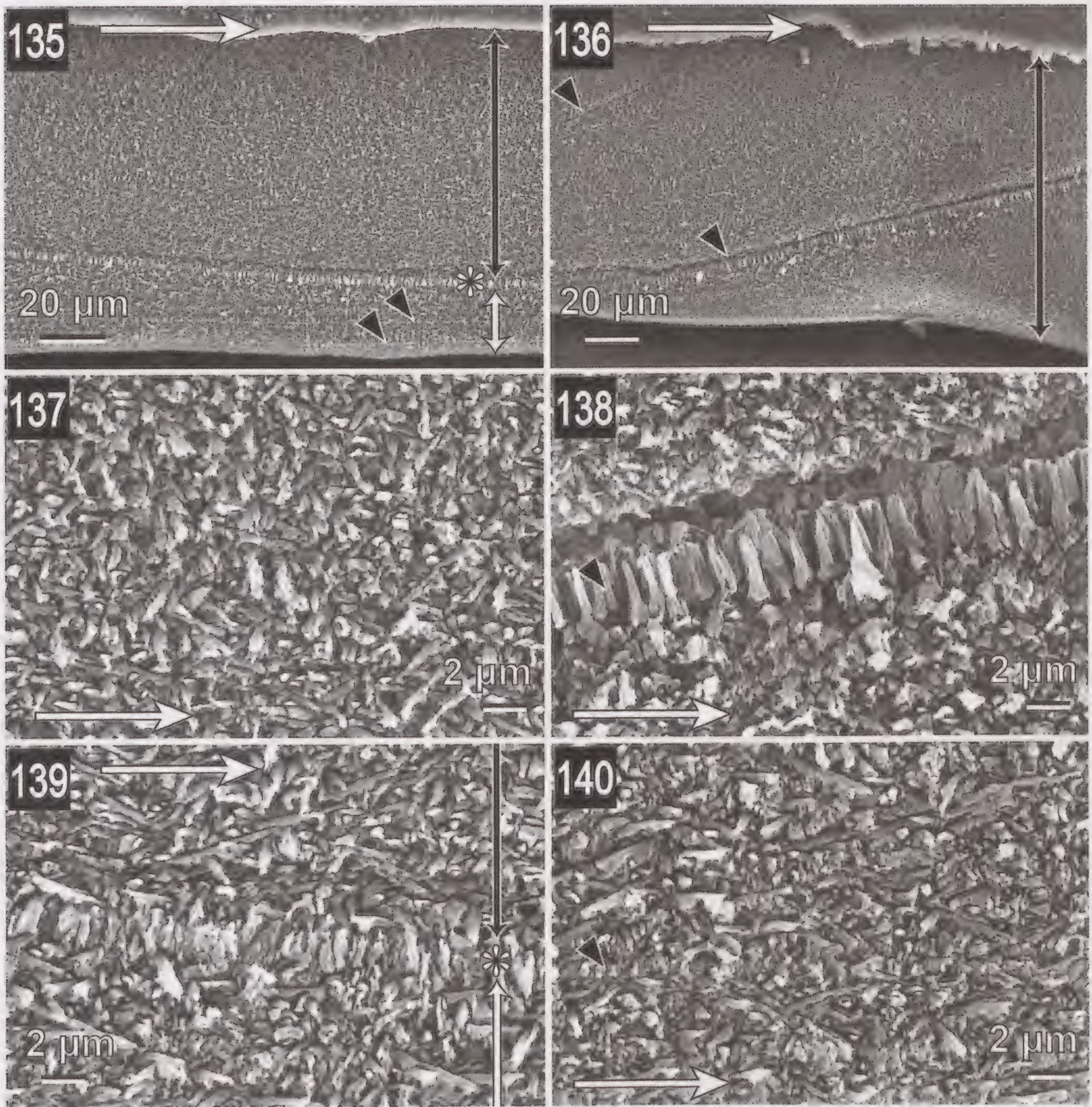
Superfamily Nuculanoidea  
Family Nuculanidae  
*Nuculana* cf. *soyoe* Habe, 1958  
(Figs. 15, 146–154)

*Shell Layers*: Outer, myostracum and inner layers are present (Figs. 146–148). Granular crystals compose the homogeneous structures of both outer and inner layers and decrease in diameter inwards. The outer layer thickens ventrally. The myostracum and inner layer thickens dorsally. The shell is robust for this family and up to approximately 550  $\mu\text{m}$  thick in the observed specimen.



*Outer Layer.* Homogeneous structure (Figs. 149–151, 153) and fine complex crossed lamellar structure. The homogeneous structure is composed of granular crystals (Figs. 149, 150). The diameter of granular

crystals is around 1  $\mu\text{m}$  and decreases in size inwards, up to around 0.5  $\mu\text{m}$ . The first-order elements of the fine complex crossed lamellar structure are up to 4  $\mu\text{m}$  long in the long axes. Several growth lines

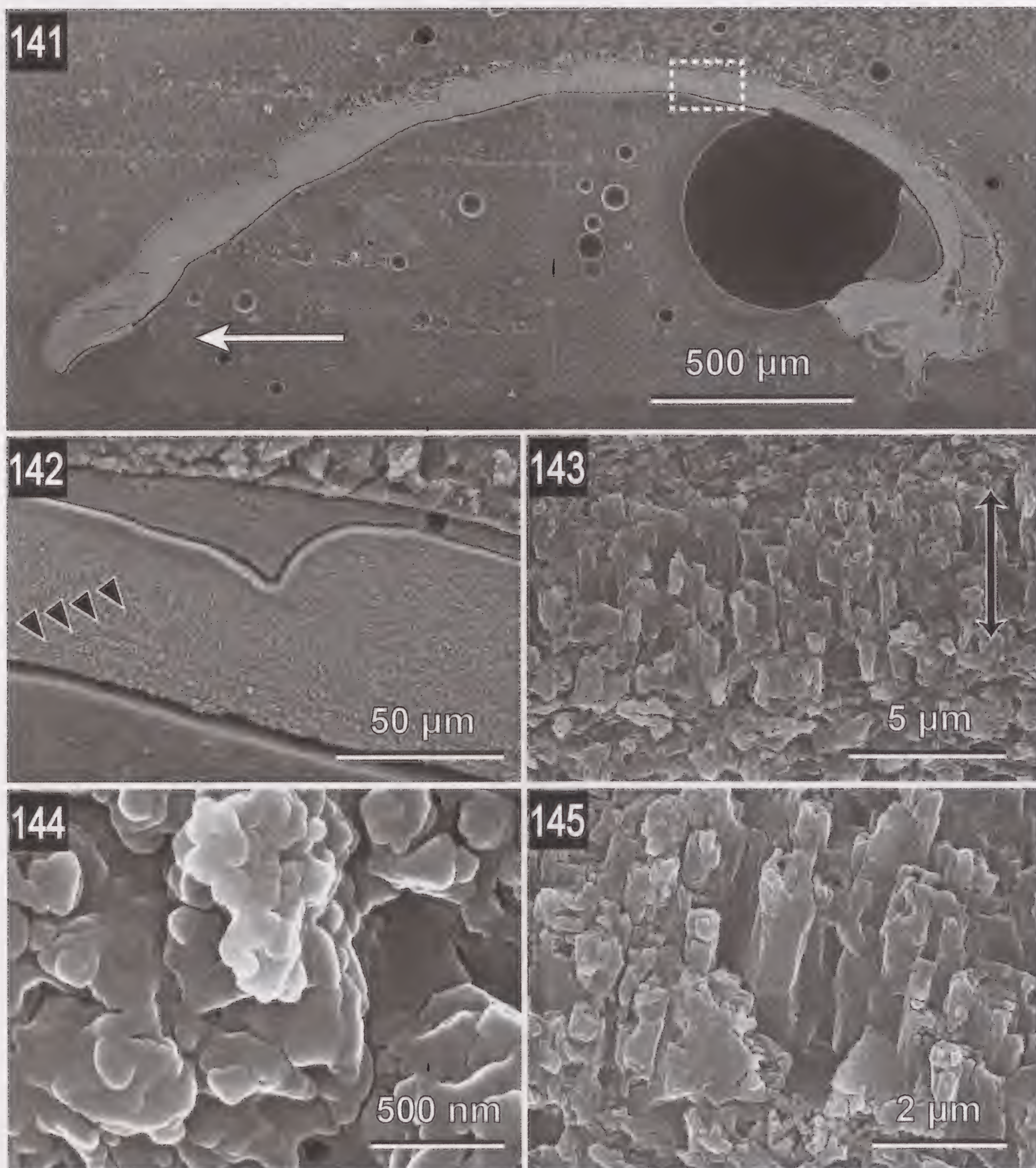


FIGS. 135–140. Scanning electron micrographs of *Setiglossa japonica* microstructure. White arrow indicate growth direction. FIG. 135: Radial section of middle part of the shell section. Black arrow, the outer layer; asterisk, myostracum; white arrow, the inner layer. Black arrow-heads indicate growth lines; FIG. 136: Radial section of ventral part of the shell section. Black arrow, the outer layer. Black arrow-heads indicate growth lines; FIG. 137: Radial section of fine complex crossed lamellar structure of the outer layer; FIG. 138: Radial section of fine complex crossed lamellar structure of the outer layer. Black arrow-head indicates growth lines; FIG. 139: Radial section which comprised of the outer, the myostracum and the inner layers. Vertical black arrow, the outer layer; asterisk, myostracum; white arrow, inner layer; FIG. 140: Radial section of fine complex crossed lamellar structure of the inner layer. Black arrow-heads indicate growth lines. FIGS. 135, 137, 139, 140: Middle part of shell; FIGS. 136, 138: Ventral part of shell.



are comprised of irregular simple prismatic structures (Fig. 151). The shape and size never change along the concave-convex surface of the shell.

*Myostracum*: Obscure to irregular simple prismatic structure (Figs. 152, 153). Irregular simple prismatic structure is recognized at the dorsal part of the shell and consists of verti-



FIGS. 141–145. Scanning electron micrographs of *Huxleyia sulcata* microstructure. White arrow indicate growth direction. FIG. 141: Radial section of shell; FIG. 142: Closer view of broken-lined square in Fig. 141 showing dorsal part of the shell section. Black arrow-head indicates growth lines; FIG. 143: Radial section of the outer layer which is comprised of homogeneous and irregular simple prismatic structures. Irregular simple prismatic structure (Black double-headed arrow) grow at growth line; FIG. 144: Radial section of homogeneous structure of the outer layer; FIG. 145: More closed image of radial section of irregular simple prismatic structure of growth line of the outer layer. FIGS. 142–145: Dorsal part of shell.



cally aligned acicular crystals. The average width of these crystals is  $0.5\ \mu\text{m}$ .

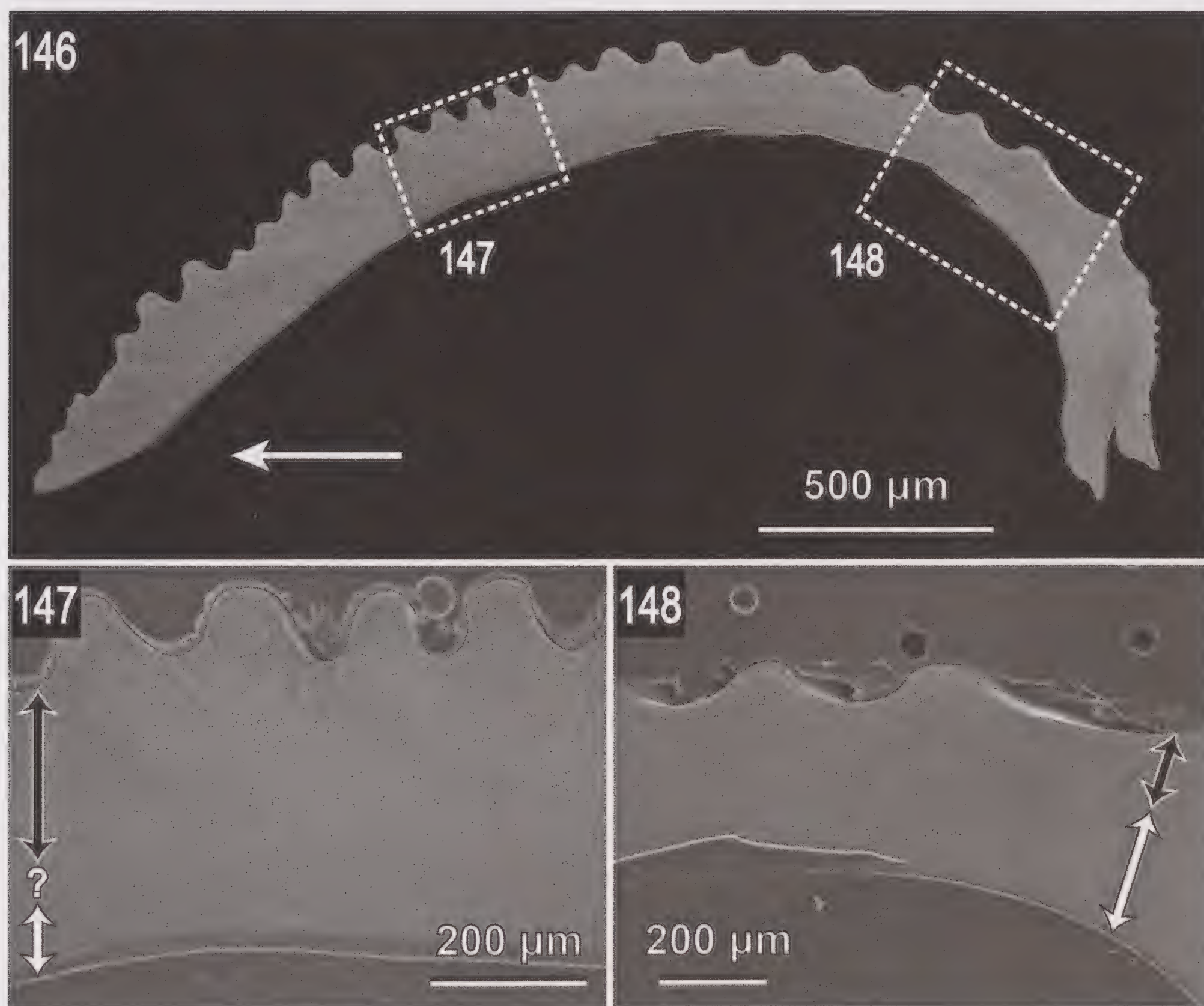
*Inner Layer:* Homogeneous structure (Figs. 152–154). Fine granular crystals (approximately  $0.2\ \mu\text{m}$ ) compose this structure. Several growth lines are composed of relatively large granular crystals.

*Nuculana tanseimaruae*  
Tsuchida & Okutani, 1985  
(Figs. 16, 155–159)

*Shell Layers:* Outer, myostracum and inner layers are present. The thickness of the inner layer is very thin. The outer layer thickens

ventrally. The inner layer generally thickens ventrally, whereas the thickest part is distributed in the middle part of a radial section. The thickness of the shells are almost constant, being approximately  $230\ \mu\text{m}$  thick in the observed specimen.

*Outer Layer:* Fibrous prismatic structure, homogeneous structure, and partly fine complex crossed lamellar structure (Figs. 156–159). Fibrous prismatic structure is distributed only in the outermost part of the shell (outer sublayer; Fig. 157). Its thickness is up to  $50\ \mu\text{m}$ . Acicular crystals comprising the fibrous prismatic structure are up to  $8\ \mu\text{m}$  long in the long axes, around  $0.7\ \mu\text{m}$  wide, and aligned vertically

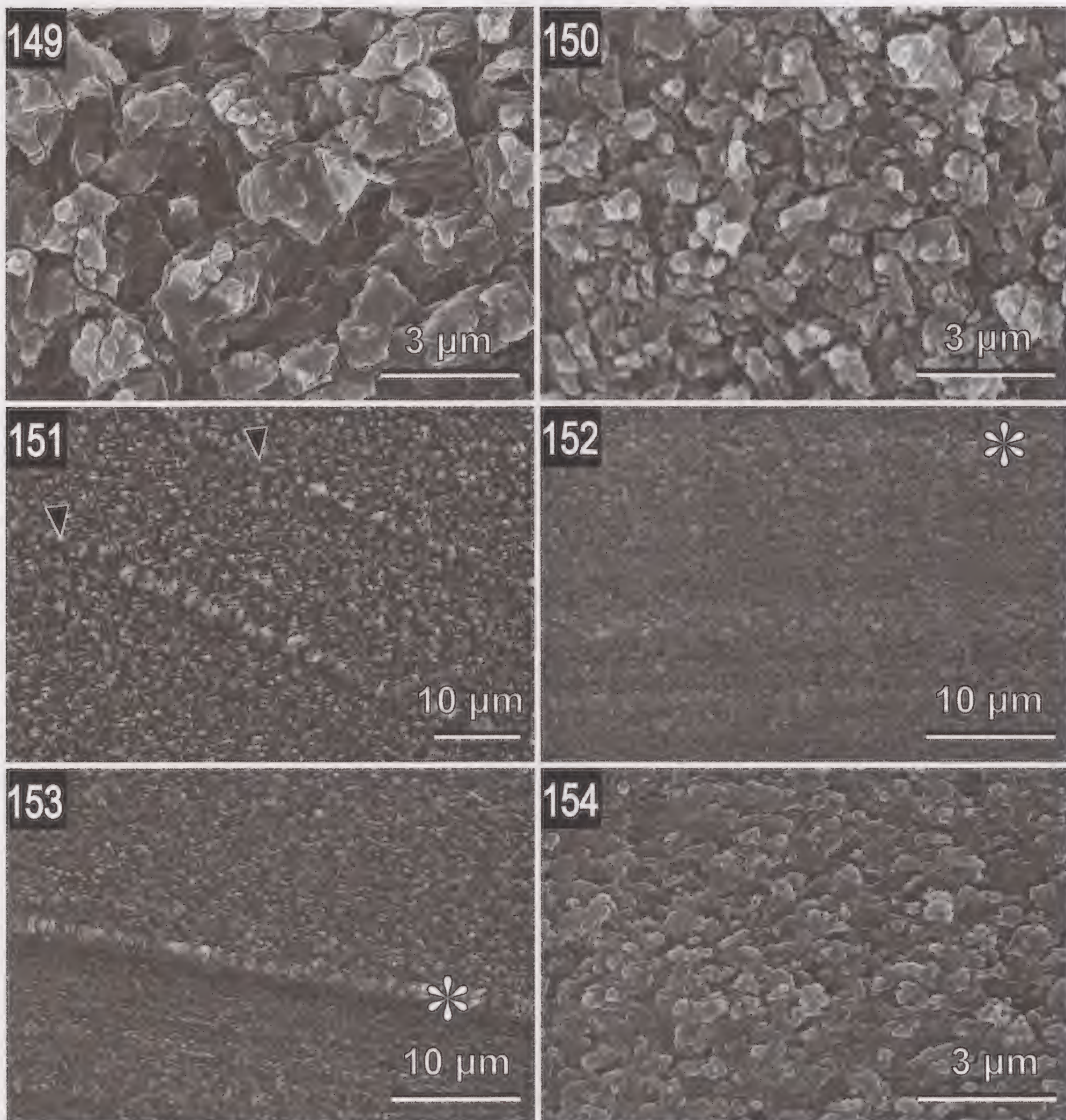


FIGS. 146–148. Scanning electron micrographs of *Nuculana* cf. *soyoae* microstructure. White arrow indicate growth direction. FIG. 146: Radial section of shell; FIG. 147: Closer view of broken-lined square in Fig. 146 showing ventral part of the shell section. Black double-headed arrow, the outer layer; white double-headed arrow, inner layer; Question mark implies obscure margin of two layers; FIG. 148: Closer view of broken-lined square in Fig. 146 showing dorsal part of the shell section. Black double-headed arrow, the outer layer; white double-headed arrow, the inner layer.



to the deposit surface. The homogeneous structure is composed of granular crystals whose diameter is around  $0.5\ \mu\text{m}$  (inner sublayer; Fig. 158). Fine complex crossed

lamellar structure is partially distributed at the ventral part of the shell where growth rings have accumulated. Acicular crystals are up to  $4\ \mu\text{m}$  long in the long axes.



FIGS. 149–154. Scanning electron micrographs of *Nuculana* cf. *soyoae* microstructure. White arrow indicate growth direction. FIG. 149: Radial section of homogeneous structure of outer part of the outer layer; FIG. 150: Radial section of homogeneous structure of inner part of the outer layer; FIG. 151: Radial section of the outer layer. Black arrow-head indicates growth lines; FIG. 152: Radial section of homogeneous structure of the inner layer. Asterisk indicates the myostracum; FIG. 153: Radial section of homogeneous structure of the inner layer at dorsal part. Asterisk indicates the myostracum; FIG. 154: Radial section of homogeneous structure of the inner layer. FIGS. 149–152: Middle part of shell; FIGS. 153, 154: Dorsal part of shell.

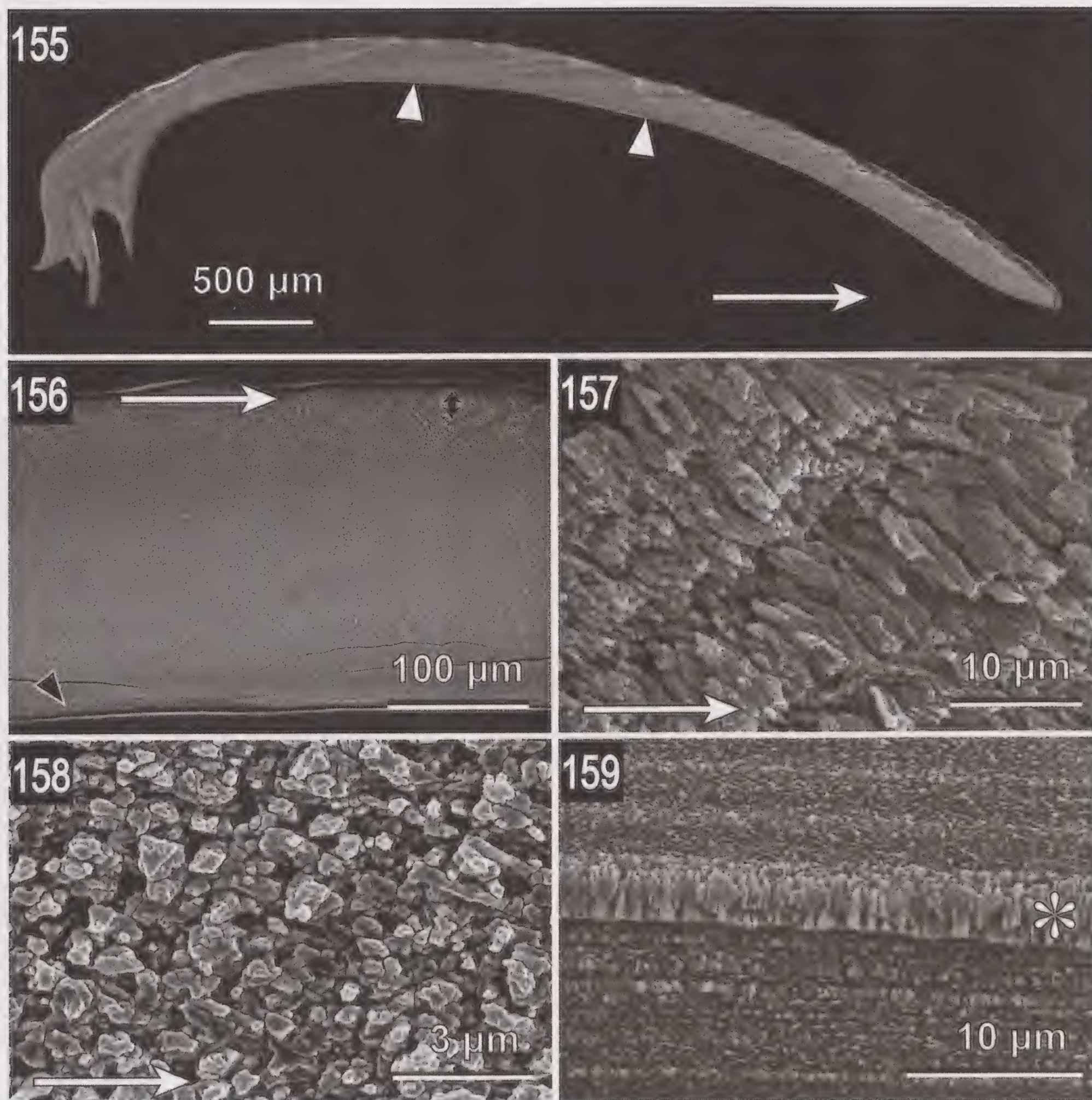


*Myostracum*: Irregular simple prismatic structure (Fig. 159). Within this family of good thickness, up to 4  $\mu\text{m}$ . The average width of these crystals is 0.4  $\mu\text{m}$ .

*Inner Layer*: Homogeneous structure (Fig. 159). Fine granular crystals of this structure are less than 0.3  $\mu\text{m}$  wide. Growth lines in this layer consist of irregular simple prismatic structures.

*Nuculana acinacea*  
Habe, 1958  
(Figs. 17, 160–163)

*Shell Layers*: Outer and inner layers are present (Fig. 160). The outer and inner layers thicken ventrally. The shell is up to approximately 280  $\mu\text{m}$  thick in the observed specimen.



FIGS. 155–159. Scanning electron micrographs of *Nuculana tanseimaruae* microstructure. White arrow indicate growth direction. FIG. 155: Radial section of shell. White arrow heads indicate the beginning of the inner layer and end of it (i.e. the inner layer distributes between these two arrow heads); FIG. 156: Radial section of the outer and myostracum. Black double-headed arrow indicates fibrous prismatic structure and black arrow head indicates the myostracum; FIG. 157: Radial section of fibrous prismatic structure of the outer layer; FIG. 158: Radial section of homogeneous structure of the outer layer; FIG. 159: Radial section of the outer, myostracum and inner layers. Asterisk indicates the myostracum. FIGS. 156, 158: Middle part of shell; FIG. 157: Ventral part of shell; FIG. 159: Dorsal part of shell.



**Outer Layer:** Homogeneous structure (Figs. 161, 162). The diameter of the granular crystals is around 0.4  $\mu\text{m}$  and diminishes in size inwards, up to around 0.2  $\mu\text{m}$ . Radial ribs on the shell surface do not change the crystal size and morphology.

**Myostracum:** Obscure, but recognized as bright lines in the SEM observations with no change in crystal morphology (Fig. 162).

**Inner Layer:** Homogeneous structure (Figs. 162, 163). The diameter of granular crystals is around 0.2  $\mu\text{m}$ .

*Nuculana yokoyamai* Kuroda, 1934  
(Figs. 18, 164–167)

**Shell Layers:** Outer and inner layers are present (Fig. 164). Both the inner and outer layers thicken ventrally. The shell is up to approximately 352  $\mu\text{m}$  thick in the observed specimen.

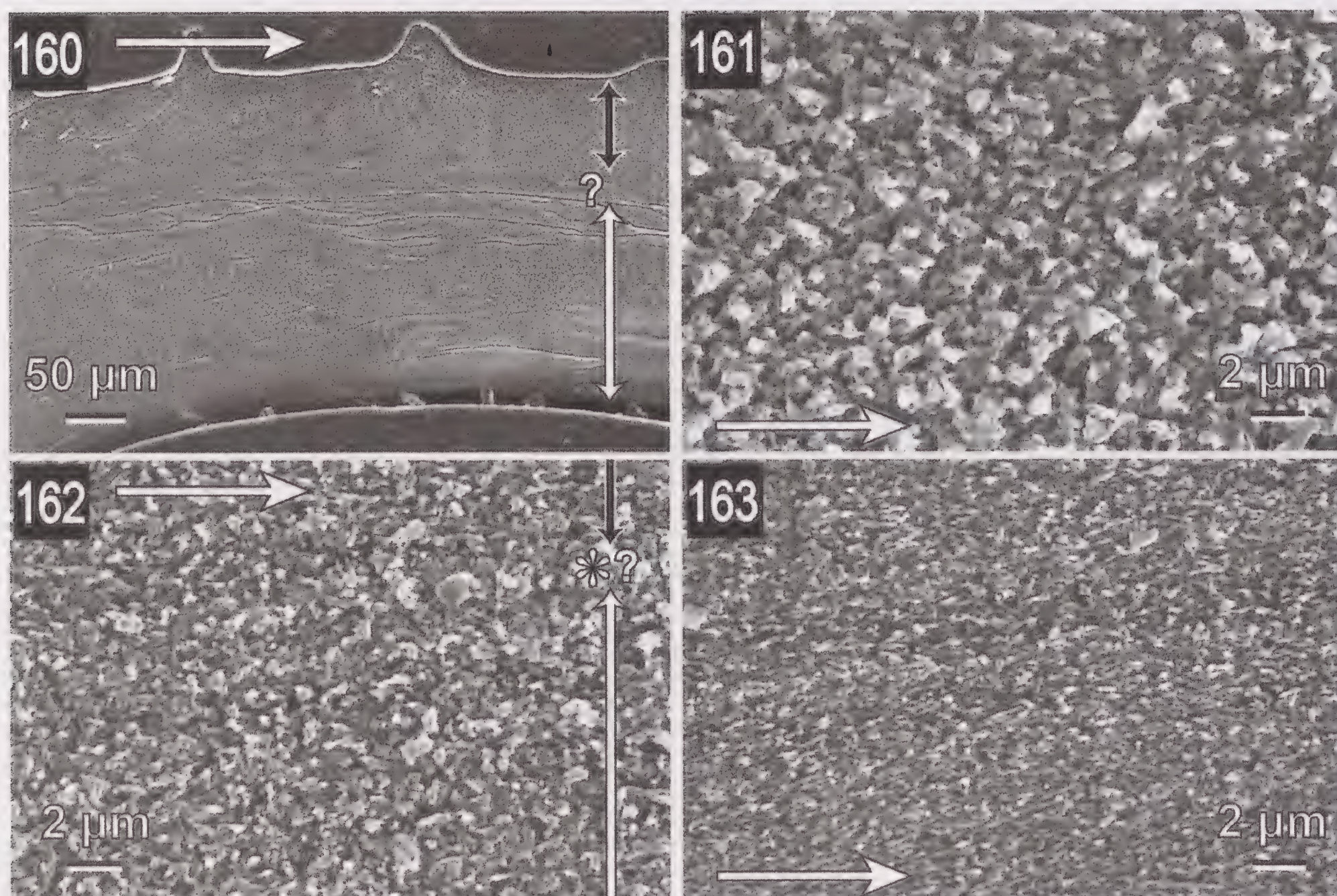
**Outer Layer:** Homogeneous structure (Figs. 164–166). Granular crystals or partly acicular

crystals compose this layer. The diameter of the granular crystals is around 0.5  $\mu\text{m}$ , and they slowly decrease in size inwards, up to around 0.3  $\mu\text{m}$ . The radial ribs on the shell surface do not alter the crystal size and morphology. Growth lines are recognized as bright lines in the observation using SEM, while the crystal morphology is not altered.

**Inner Layer:** Homogeneous structure (Figs. 166, 167). The diameter of granular crystals is around 0.3  $\mu\text{m}$ . Growth lines are recognized as bright lines in the observation using SEM, while the crystal morphology is constant.

*Nuculana gordonis* (Yokoyama, 1920)  
(Figs. 19, 168–172)

**Shell Layers:** Outer, myostracum and inner layers are present (Figs. 168, 169). The outer and inner layers thicken ventrally. The shell is up to approximately 148  $\mu\text{m}$  thick in the observed specimen.



FIGS. 160–163. Scanning electron micrographs of *Nuculana acinacea* microstructure. White arrow indicate growth direction. FIG. 160: Radial section of dorsal part of the shell section. Black arrow, the outer layer; question mark, probable position of the myostracum; white arrow, the inner layer; FIG. 161: Radial section of homogeneous structure of the outer layer; FIG. 162: Radial section of the outer, myostracum and inner layers. Vertical black arrow indicates the outer layer. Asterisk shows the myostracum and white arrow is the inner layer; FIG. 163: Radial section of homogeneous structure of the inner layer. FIGS. 160–163: Dorsal part of shell.



**Outer Layer:** Fibrous prismatic (Fig. 170) and homogeneous structure (Fig. 171). Fibrous prismatic structure in the outer sublayer of the outer layer is distributed only in the outermost part of the shell. The thickness of the outer sublayer is up to 14  $\mu\text{m}$ . Acicular crystals composing the outer sublayer are up to 4  $\mu\text{m}$  long in the long axes, around 0.4 to 4  $\mu\text{m}$  wide, and recline at angles of approximately  $55^\circ$  against the growth direction in a radial section. The inner sublayer of the outer layer consists of a homogeneous structure, whose granular crystals are 0.7  $\mu\text{m}$  in diameter. Acicular crystals partly grow up to 6  $\mu\text{m}$  long in the long axes and form fine complex crossed lamellar structures in the inner sublayer.

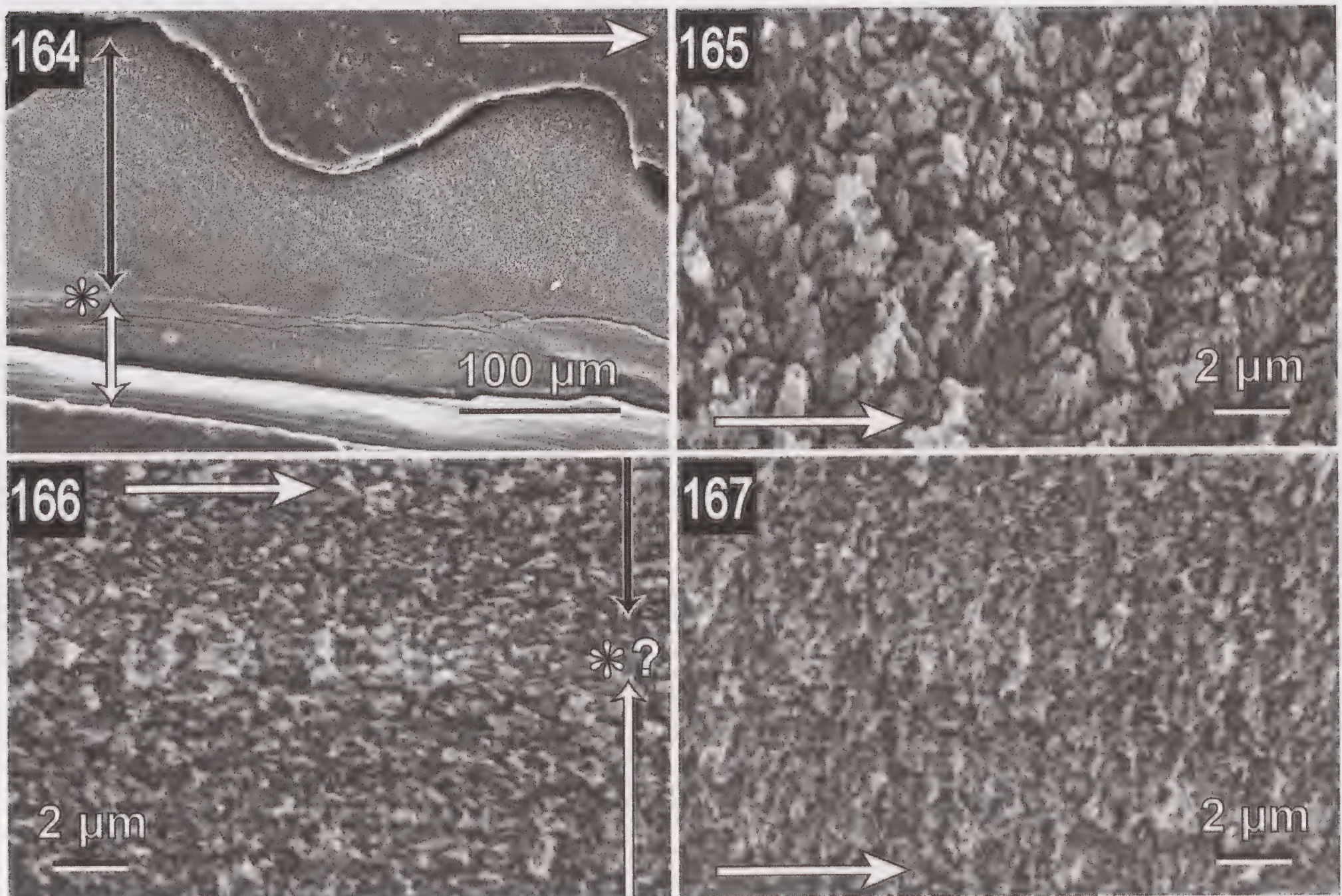
**Myostracum:** Generally obscure, partly irregular simple prismatic structure (Fig. 172). The average width of acicular crystals in the irregular simple prismatic structure is less than 0.5  $\mu\text{m}$ .

**Inner Layer:** Homogeneous structure (Fig. 172) and partly fine complex crossed lamellar structure. The diameter of the granular crystals is around 0.3  $\mu\text{m}$ . Growth lines are recognized as bright lines in the observation using SEM, while no change in crystal morphology is recognized.

Family Bathyspinulidae  
*Bathyspinula calcarella* (Dall, 1908)  
 (Figs. 20, 173–178)

**Shell Layers:** Outer and inner layers are present (Fig. 173). The myostracum is obscure. The outer layer thickens ventrally and the inner layer thicken dorsally. The shell is up to approximately 240  $\mu\text{m}$  thick in the observed specimen.

**Outer Layer:** Fibrous prismatic structure (outer sublayer; Fig. 174), homogeneous structure, and partly fine complex crossed lamellar structure (inner sublayer; Figs. 175–177).

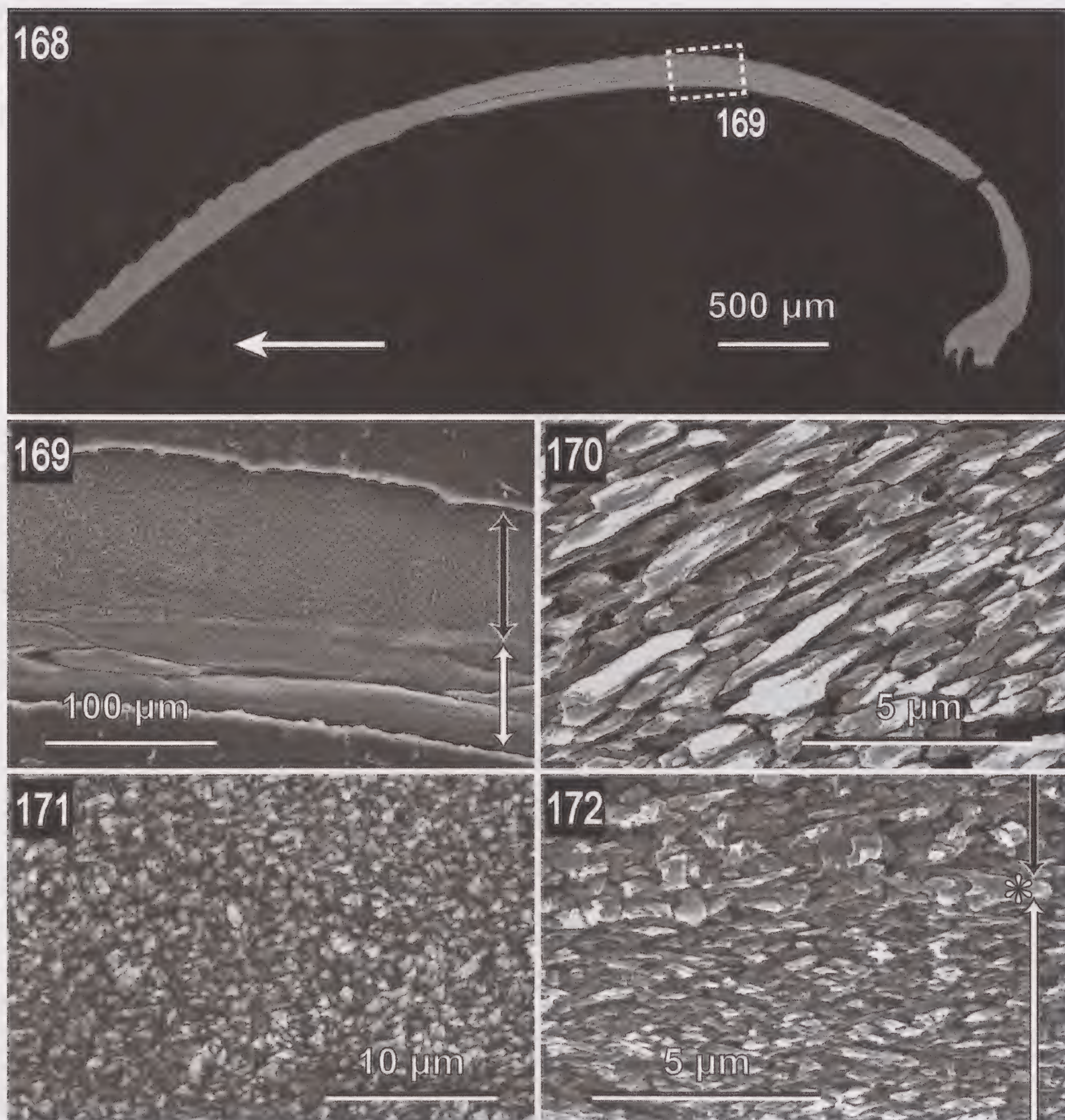


FIGS. 164–167. Scanning electron micrographs of *Nuculana yokoyamai* microstructure. White arrow indicate growth direction. FIG. 164: Radial section of middle part of the shell section. Black arrow, the outer layer; asterisk, myostracum; white arrow, the inner layer; FIG. 165: Radial section of homogeneous structure of the outer layer; FIG. 166: Radial section of homogeneous structure of the outer, myostracum and inner layers. Vertical black arrow indicates the outer layer. Asterisk shows the myostracum and white arrow is the inner layer. FIG. 167: Radial section of homogeneous structure of the inner layer. FIGS. 164–167: Middle part of shell.



The thickness of the outer sublayer is up to 30  $\mu\text{m}$ . Acicular crystals that compose the outer sublayer are up to 4  $\mu\text{m}$  long in the long axes, around 0.4  $\mu\text{m}$  in width, and recline at angles of approximately  $45^\circ$  against the growth direction in a radial section. Crystals composing the outer layer

decrease in size inwards and their morphology changes from acicular to granular crystals in the inner sublayer. Granular crystals are around 0.4 in diameter. A fine complex crossed lamellar structure is irregularly distributed in the inner sublayer (Figs. 175, 176).

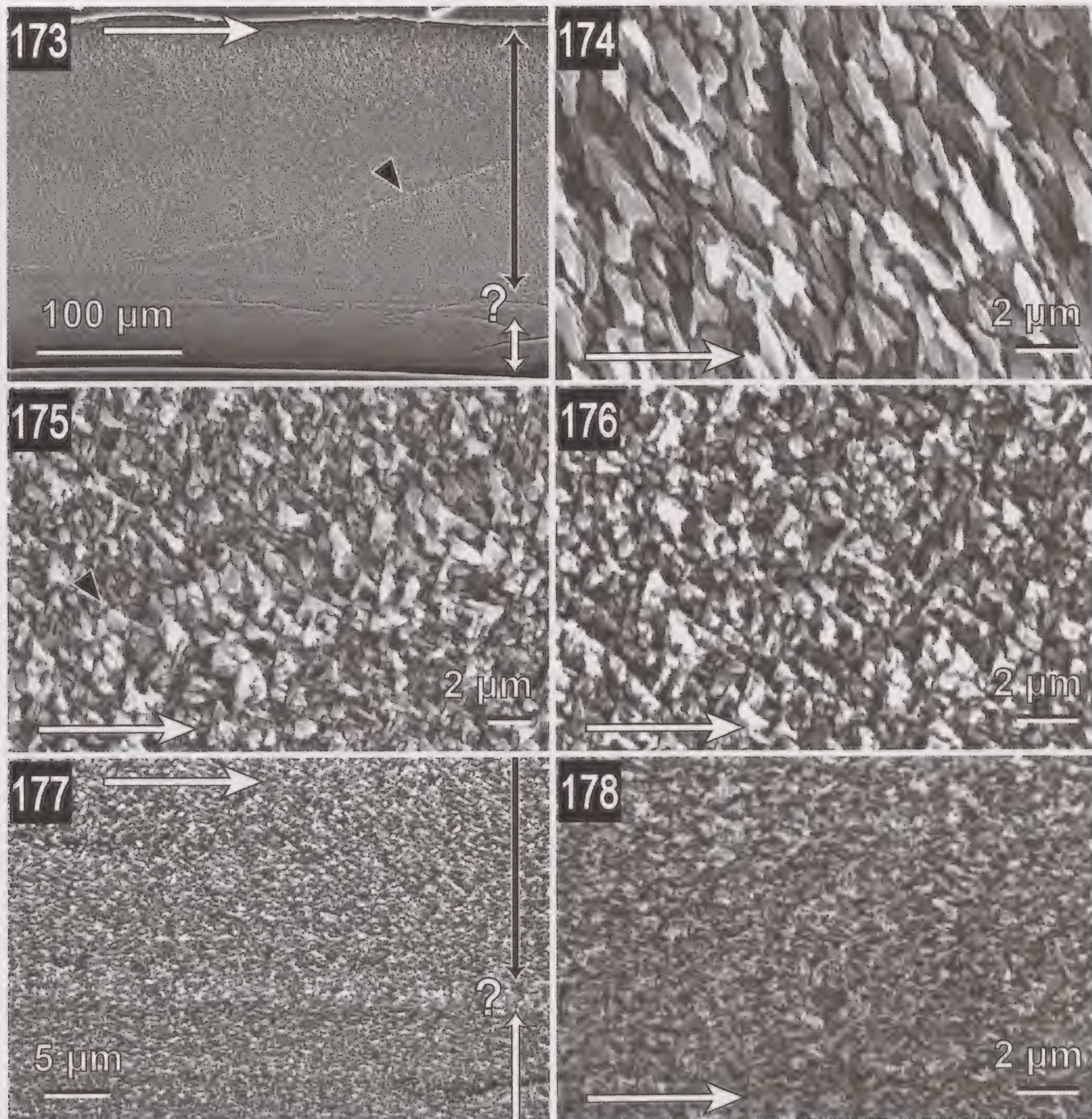


FIGS. 168–172. Scanning electron micrographs of *Nuculana gordonis* microstructure. Horizontal white arrow indicate growth direction. FIG. 168: Radial section of shell; FIG. 169: Closer view of broken-lined square in Fig. 168 showing dorsal part of the shell section. Black double-headed arrow, the outer layer; white double-headed arrow, the inner layer; FIG. 170: Radial section of fibrous prismatic structure of the outer sublayer of the outer layer; FIG. 171: Radial section of homogeneous structure of the inner sublayer of the outer layer; FIG. 172: Radial section of the outer, myostracum and inner layers. Vertical black double-headed arrow, the outer layer; asterisk, the myostracum; white double-headed arrow, the inner layer. FIGS. 169–172: Middle part of shell.



*Myostracum*: Obscure but recognized as bright lines in the observation using SEM, while crystal morphology is not altered (Figs. 173, 177).

*Inner Layer*. Homogeneous structure (Figs. 177, 178). Very fine granular crystals compose this layer and they are less than  $0.3\ \mu\text{m}$  in diameter.



FIGS. 173–178. Scanning electron micrographs of *Bathyspinula calcarella* microstructure. Horizontal white arrow indicate growth direction. FIG. 173: Radial section of middle part of the shell section. Black arrow, the outer layer; question mark, probable position of the myostracum; white arrow, the inner layer. Black arrow head indicates the myostracum; FIG. 174: Radial section of fibrous prismatic structure of the outer sublayer of the outer layer; FIG. 175: Radial section of fine complex crossed lamellar to homogeneous structure of the inner sublayer of the outer layer. Black arrow head indicates the myostracum; FIG. 176: Radial section of fine complex crossed lamellar to homogeneous structure of the inner sublayer of the outer layer; FIG. 177: Radial section of the outer, myostracum and inner layers. Vertical black double-headed arrow, the outer layer; question mark, probable position of the myostracum; white double-headed arrow, the inner layer; FIG. 178: Radial section of homogeneous structure of the inner layer. FIGS. 173–178: Middle part of shell.

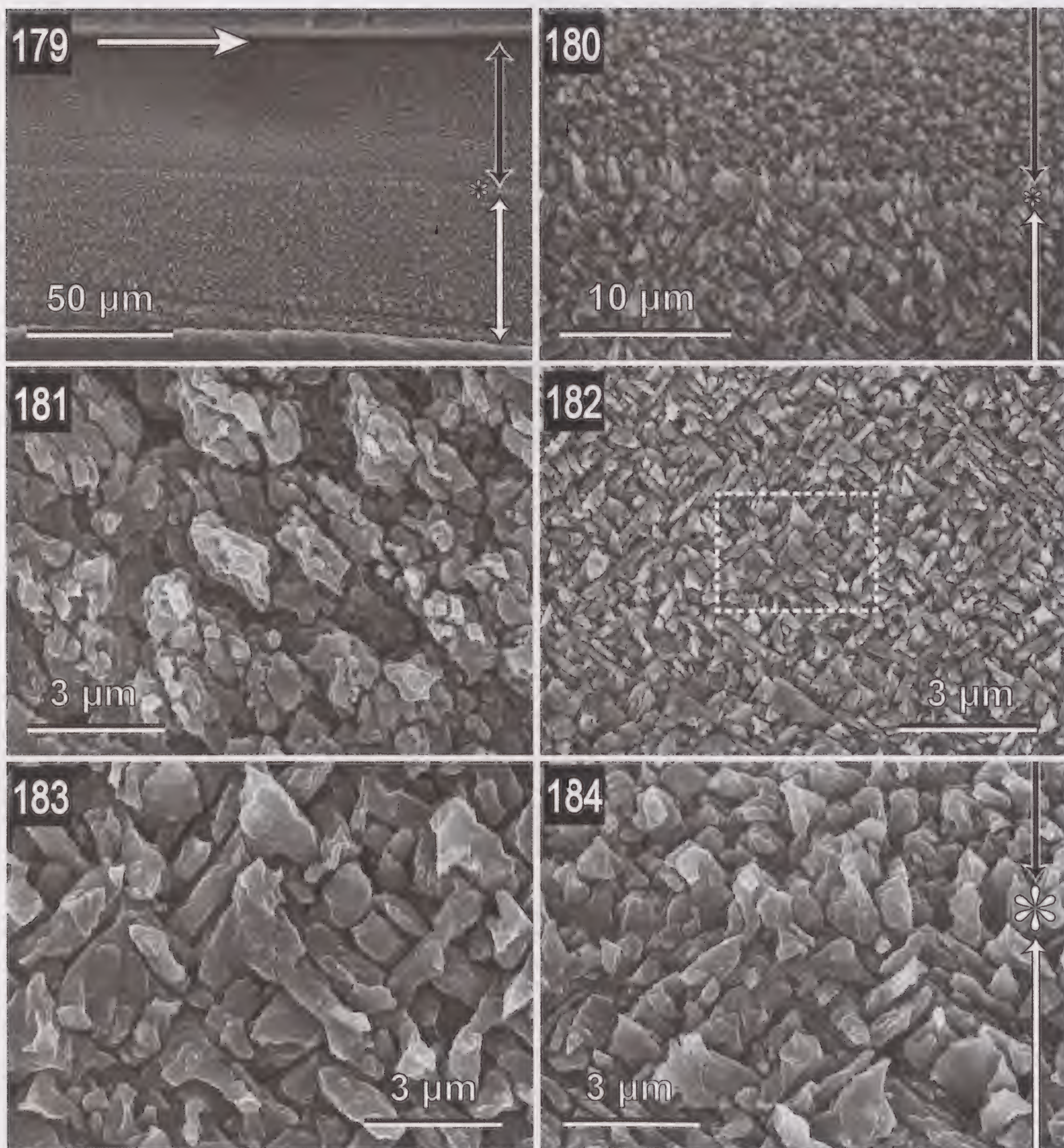


Family Malletiidae  
*Malletia takaii* Okutani, 1968  
 (Figs. 21, 179–184)

*Shell Layers:* Outer, myostracum and inner layers are present (Fig. 179). Both the outer

and inner layers thicken ventrally. The shell is up to approximately 125  $\mu\text{m}$  thick in the observed specimen.

*Outer Layer:* Homogeneous structure (Figs. 179–181). Granular crystals consisting of homogeneous structure decrease in diameter inwards



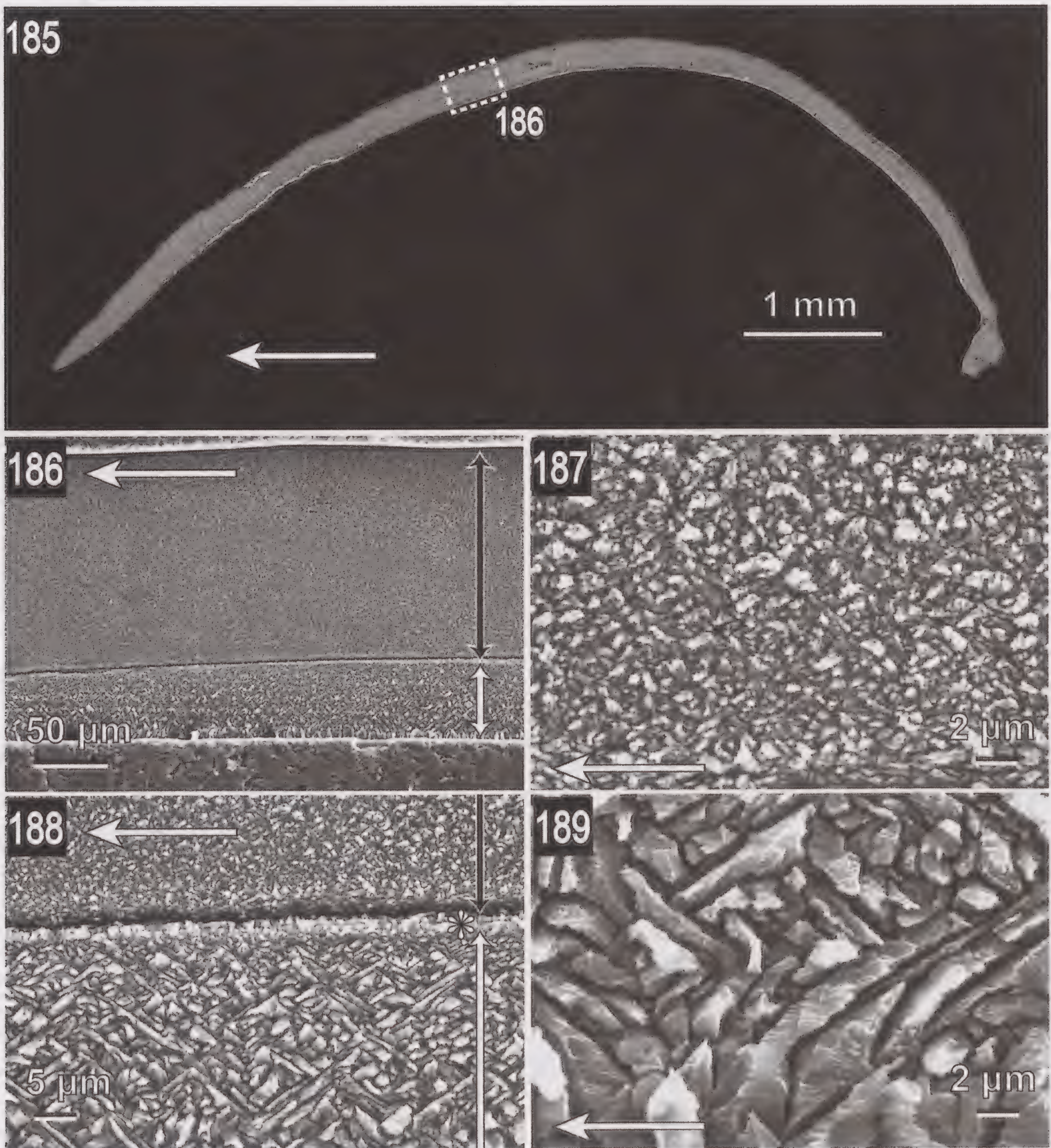
FIGS. 179–184. Scanning electron micrographs of *Malletia takaii* microstructure. Horizontal white arrow indicate growth direction; FIG. 179: Radial section of the outer, myostracum and inner layers. Vertical black double-headed arrow, the outer layer; asterisk, the myostracum; white double-headed arrow, the inner layer; FIG. 180: Closer view of Fig. 179; FIG. 181: Radial section of homogeneous structure of the outer layer; FIG. 182: Radial section of fine complex crossed lamellar structure of the inner layer; FIG. 183: Closer view of broken-lined square in Fig. 182 showing acicular crystals of the inner layer; FIG. 184: Closer view of radial section of the outer, myostracum and inner layers. Vertical black double-headed arrow, the outer layer; asterisk, the myostracum; white double-headed arrow, the inner layer.



(from 1 to 0.7  $\mu\text{m}$ ). Second-order crystals are less than 200 nm in diameter (Fig. 181).

*Myostracum*: Irregular simple prismatic structure consisting of vertically aligned acicular crystals (Figs. 180, 184). The average width of these crystals is 0.6  $\mu\text{m}$ .

*Inner Layer*. Fine complex crossed lamellar structure (Figs. 180, 182–184). Acicular crystals composing first-order lamellae of fine complex crossed lamellar structure are around 0.7  $\mu\text{m}$  wide, up to 7  $\mu\text{m}$  long in the long axes, and inclined at around  $35^\circ$  to the deposit surface.



FIGS. 185–189. Scanning electron micrographs of *Malletia humilior* microstructure. Horizontal white arrow indicate growth direction. FIG. 185: Radial section of shell; FIG. 186: Closer view of broken-lined square in Fig. 185 showing middle part of the shell section. Black double-headed arrow, the outer layer; white double-headed arrow, inner layer; FIG. 187: Radial section of homogeneous structure of the outer layer; FIG. 188: Radial section of the outer, myostracum and inner layers. Vertical black double-headed arrow, the outer layer; asterisk, the myostracum; white double-headed arrow, the inner layer; FIG. 189: Radial section of fine complex crossed lamellar structure of the inner layer. FIGS. 186–189: Middle part of shell.



*Malletia humilior* Prashad, 1932  
(Figs. 22, 185–189)

**Shell Layers:** Outer, myostracum and inner layers are present (Figs. 185–189). The outer layer thickens ventrally. The inner layer generally thickens ventrally, while its thickest part is at the middle. The shell has almost constant thickness and is approximately 256  $\mu\text{m}$  thick in the observed specimen.

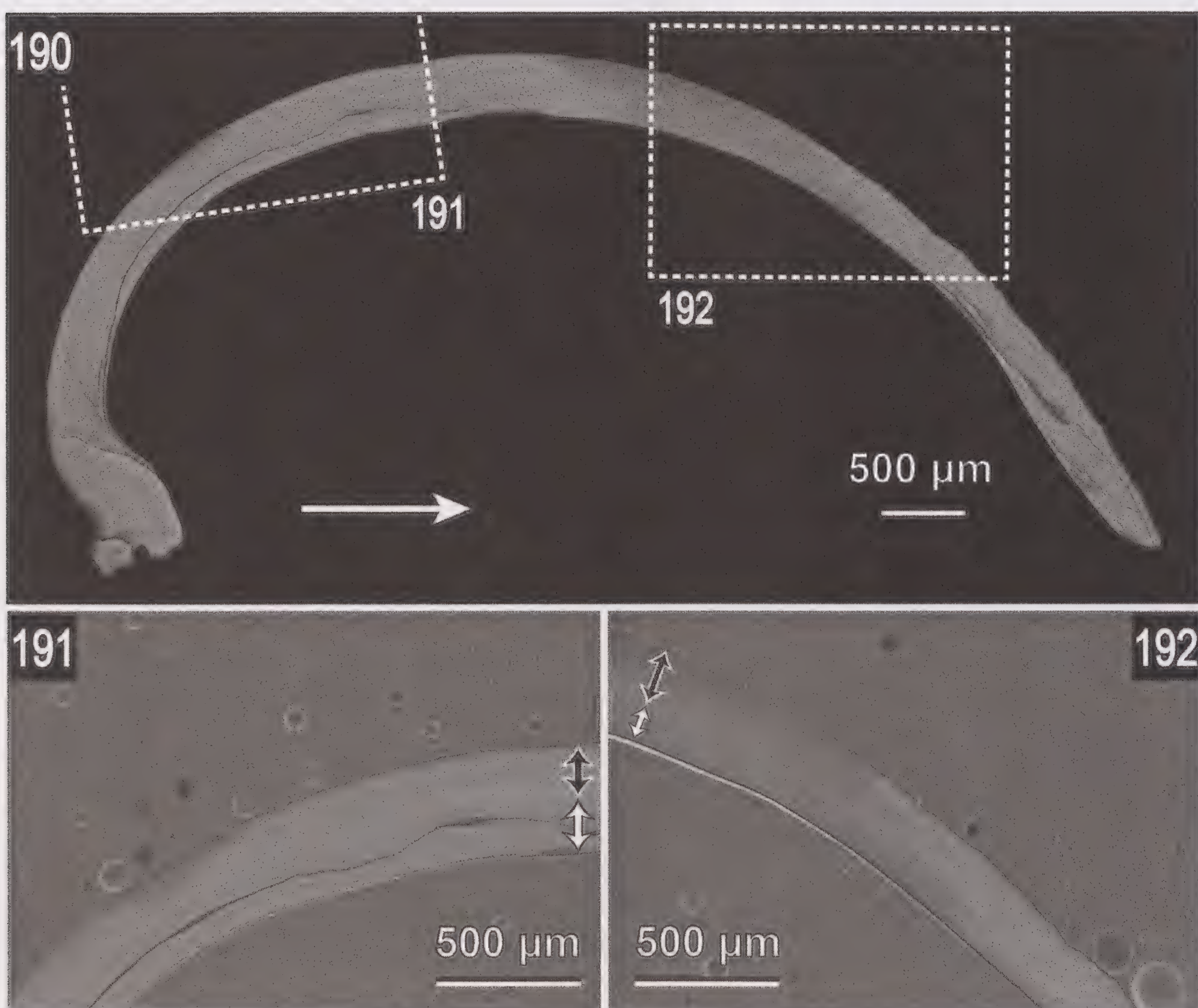
**Outer Layer:** Homogeneous structure (Figs. 186–188). Granular crystals with homogeneous structure are 0.5  $\mu\text{m}$  in diameter.

**Myostracum:** Irregular simple prismatic structure consisting of vertically aligned acicular crystals (Figs. 186–188). The average width of these crystals is 1  $\mu\text{m}$ .

**Inner layer:** Fine complex crossed lamellar structure (Figs. 188, 189). Acicular crystals composing first-order lamellae of fine complex crossed lamellar structure are inclined at around  $40^\circ$  degree to deposit surface. Acicular crystals enlarge inwards. At the outermost part, crystals are around 0.8  $\mu\text{m}$  wide and 5  $\mu\text{m}$  long in the long axes. At the innermost part, crystals are around 1.8  $\mu\text{m}$  in width and 18  $\mu\text{m}$  in length.

Family Neilonellidae  
*Neilonella soyoae* Habe, 1958  
(Figs. 23, 190–196)

**Shell Layers:** Outer and inner layers are present (Figs. 190–192). The myostracum is obscure. The outer and inner layers thicken



FIGS. 190–192. Scanning electron micrographs of *Neilonella soyoae* microstructure. Horizontal white arrow indicate growth direction. FIG. 190: Radial section of shell; FIG. 191: Closer view of broken-lined square in Fig. 190 showing dorsal part of the shell section. Black double-headed arrow, the outer layer; white double-headed arrow, inner layer; FIG. 192: Closer view of broken-lined square in Fig. 190 showing ventral part of the shell section. Black double-headed arrow, the outer layer; white double-headed arrow, inner layer.



ventrally. The shell is up to approximately 380  $\mu\text{m}$  thick in the observed specimen.

**Outer Layer.** Fibrous prismatic structure in the outer sublayer (Fig. 193) and homogeneous structure in the inner sublayer (Figs. 194, 195). The thickness of the outer sublayer is up to 65  $\mu\text{m}$ . Acicular crystals composing the outer sublayer are up to 6  $\mu\text{m}$  long in the long axes, around 0.5  $\mu\text{m}$  in width, and recline at an angle of approximately  $50^\circ$  against the growth direction in a radial section. The homogeneous structure is composed of granular crystals (Figs. 194, 195). The average diameter of the granular crystals is around 0.5  $\mu\text{m}$  and they diminish in size inwards, up to around 0.3  $\mu\text{m}$ .

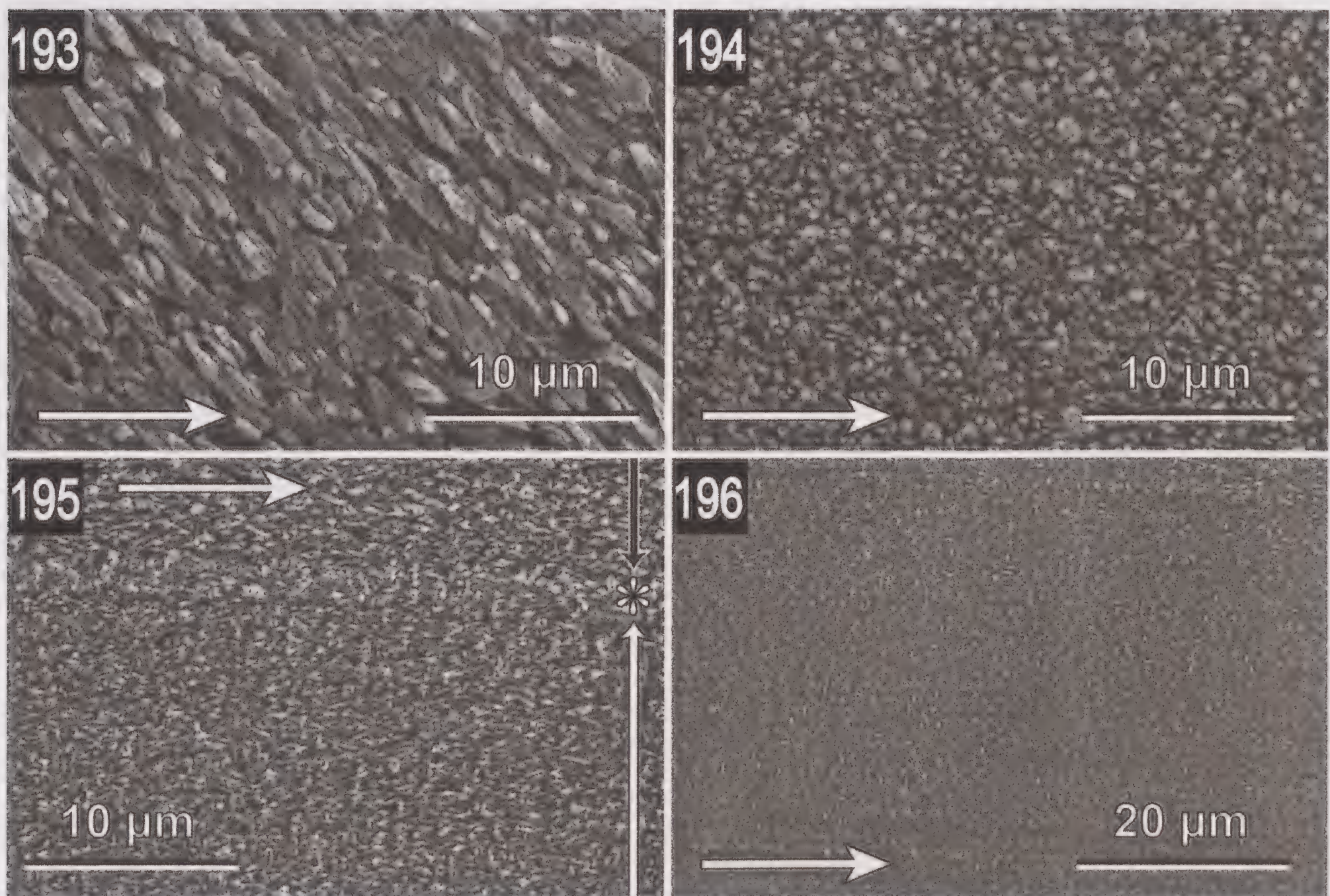
**Myostracum:** Obscure, but recognized as bright lines in the SEM observations with no change in crystal morphology (Fig. 195).

**Inner Layer.** Homogeneous structure (Figs. 195, 196). Very fine granular crystals that are less than 0.2  $\mu\text{m}$  in diameter compose this layer.

*Neilonella dubia* Prashad, 1932  
(Figs. 24, 197–200)

**Shell Layers:** Outer, myostracum and inner layers are present. The outer layer thickens ventrally. The inner layer generally thickens ventrally but it distributed in the middle part of a radial section. The shell is up to approximately 203  $\mu\text{m}$  thick in the observed specimen.

**Outer Layer.** Fibrous prismatic (outer sublayer; Fig. 197) and homogeneous structure (inner sublayer; Figs. 198, 199). The thickness of the outer sublayer is up to 16  $\mu\text{m}$ . Acicular crystals composing the outer sublayer are up to 8  $\mu\text{m}$  long in the long axes, around 0.6  $\mu\text{m}$  in width, and recline at angles of approximately  $35^\circ$  against the growth direction in a radial section (Fig. 197). The homogeneous structure is composed of granular crystals (Figs. 198, 199). The average diameter of



FIGS. 193–196. Scanning electron micrographs of *Neilonella soyoae* microstructure. Horizontal white arrow indicate growth direction. FIG. 193: Radial section of fibrous prismatic structure of the outer sublayer of the outer layer; FIG. 194: Radial section of homogeneous structure of the inner sublayer of the outer layer; FIG. 195: Radial section of the outer, myostracum and inner layers. Vertical black double-headed arrow, the outer layer; asterisk, the myostracum; white double-headed arrow, the inner layer; FIG. 196: Radial section of homogeneous structure of the inner layer. FIGS. 193, 194: Ventral part of shell; FIGS. 195, 196: Middle part of shell.



the granular crystals is around 1  $\mu\text{m}$  and they diminish in size inwards, up to around 0.5  $\mu\text{m}$ .

*Myostracum*: Irregular simple prismatic structure consisting of vertically aligned acicular crystals (Fig. 199). The average width of these crystals is 0.3  $\mu\text{m}$ .

*Inner Layer*: Homogeneous structure (Figs. 199, 200). Very fine granular crystals that are less than 0.2  $\mu\text{m}$  in diameter form this layer.

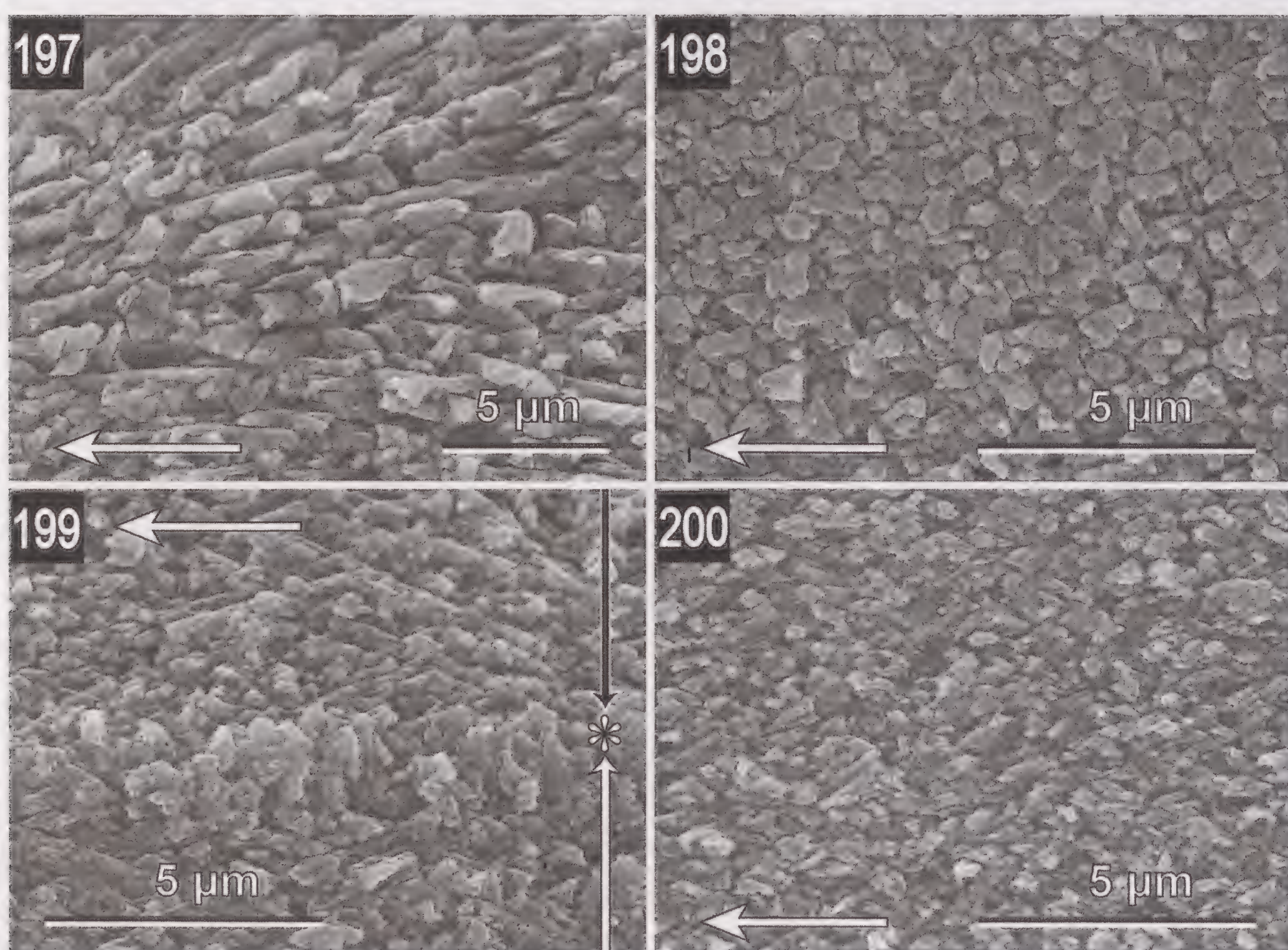
*Neilonella kirai* Habe, 1953  
(Figs. 25, 201–205)

*Shell Layers*: Outer, myostracum and inner layers are present (Fig. 201). The outer and inner layers thicken dorsally. The shell is up to approximately 400  $\mu\text{m}$  thick in the observed specimen.

*Outer Layer*: Fibrous prismatic (outer sublayer; Fig. 202) and homogeneous structures (inner sublayer; Figs. 203, 204). The thickness of the outer sublayer is up to 110  $\mu\text{m}$ . Acicular crystals consisting of the outer sublayer are up to 5  $\mu\text{m}$  long in the long axes and around 0.8  $\mu\text{m}$  in width, and recline at an angle of approximately 50° against the growth direction in a radial section. The homogeneous structure is composed of granular crystals. The average diameter of the granular crystals is around 0.6  $\mu\text{m}$  and they diminish in size inwards, up to around 0.4  $\mu\text{m}$ .

*Myostracum*: Irregular simple prismatic structure consisting of vertically aligned acicular crystals (Figs. 203, 204). The average width of these crystals is 0.2  $\mu\text{m}$ .

*Inner Layer*: Homogeneous structure (Figs. 203–205). Very fine granular crystals are less than 0.2  $\mu\text{m}$  in diameter.



FIGS. 197–200. Scanning electron micrographs of *Neilonella dubia* microstructure. Horizontal white arrow indicate growth direction. FIG. 197: Radial section of fibrous prismatic structure of the outer sublayer of the outer layer; FIG. 198: Radial section of homogeneous structure of the inner sublayer of the outer layer; FIG. 199: Radial section of the outer, myostracum and inner layers. Vertical black double-headed arrow, the outer layer; asterisk, the myostracum; white double-headed arrow, the inner layer; FIG. 200: Radial section of homogeneous structure of the inner layer. FIGS. 197–200: Dorsal part of shell.

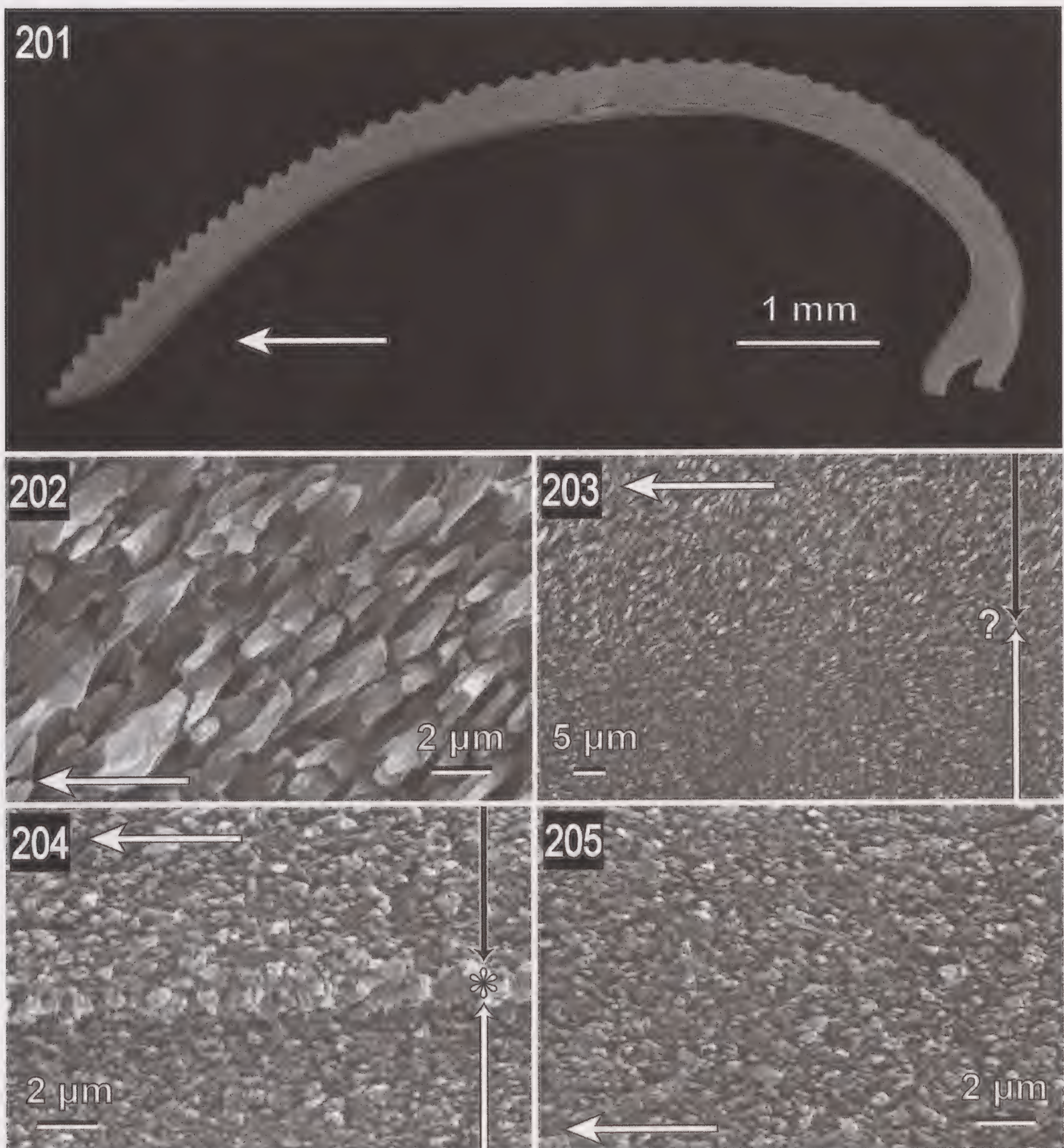


Family Tindariidae  
*Tindaria soyoae* Habe, 1953  
 (Figs. 26, 206–209)

*Shell Layers:* Outer, myostracum and inner layers are present (Fig. 206). The outer and

inner layers thicken ventrally. The shell is up to approximately 280  $\mu\text{m}$  thick in the observed specimen.

*Outer Layer:* Homogeneous structure (Figs. 206–208). The diameter of the granular crystals is around 1.2  $\mu\text{m}$  and they diminish



FIGS. 201–205. Scanning electron micrographs of *Neilonella kirai* microstructure. Horizontal white arrow indicate growth direction. FIG. 201: Radial section of shell; FIG. 202: Radial section of fibrous prismatic structure of the outer sublayer of the outer layer; FIG. 203: Radial section of the outer, myostracum and inner layers. Vertical black double-headed arrow, the outer layer; question mark, probable position of the myostracum; white double-headed arrow, the inner layer; FIG. 204: Radial section of the outer, myostracum and inner layers. Vertical black double-headed arrow, the outer layer; asterisk, probable position of the myostracum; white double-headed arrow, the inner layer; FIG. 205: Radial section of homogeneous structure of the inner layer. FIGS. 202–205: Middle part of shell.



in size inwards, up to around  $0.5\ \mu\text{m}$ . Radial ribs on the exterior surface do not alter the crystal size and morphology.

*Myostracum*: Obscure to irregular simple prismatic structure (Figs. 206, 208). Irregular prisms consist of vertically aligned acicular crystals. The average width of these crystals is  $0.5\ \mu\text{m}$ .

*Inner layer*: Homogeneous structure (Figs. 208, 209). The average diameter of the granular crystals is around  $0.5\ \mu\text{m}$ .

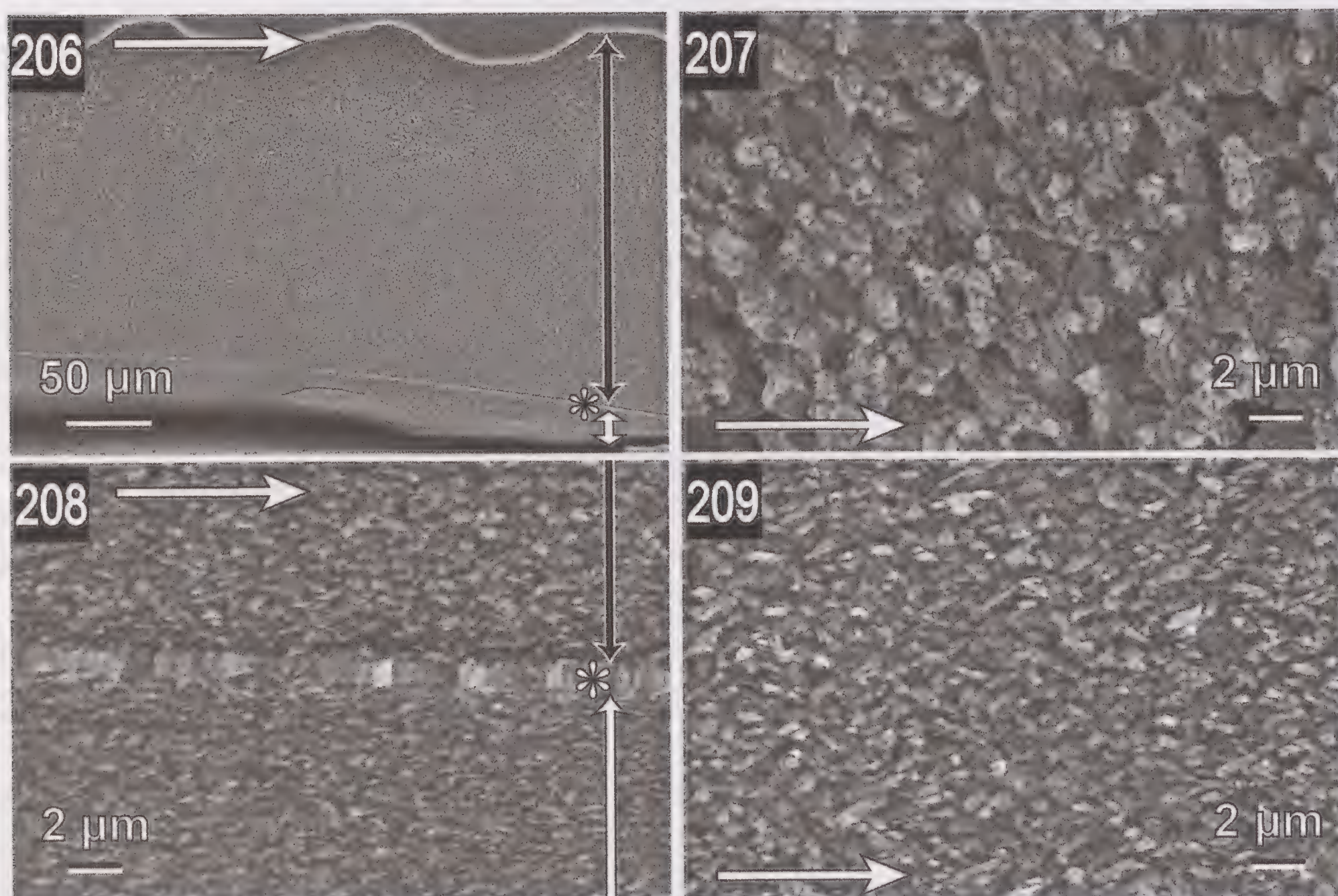
Family Yoldiidae  
*Megayoldia lischkei* (Smith, 1885)  
 (Figs. 27, 210–215)

*Shell Layers*: Outer, myostracum and inner layers are present (Fig. 210). The outer layer thickens ventrally, and the inner layer generally thickens ventrally in the middle part of a radial section. The shell is thickened in the

ventral part and is approximately  $360\ \mu\text{m}$  thick in the observed specimen.

*Outer Layer*: Generally shows a homogeneous structure (Figs. 211, 212, 214) and partly a spherulitic structure (Figs. 211, 212). Granular crystals composing the homogeneous structure are  $1.5\ \mu\text{m}$  in diameter at the outer part and diminish in size inwards, up to around  $0.6\ \mu\text{m}$  in diameter. Spherulitic structure is partly distributed along growth lines. Acicular crystals radiate equally in all directions from a central nucleation site and constitute the first-order spherulites, which are around  $3\ \mu\text{m}$  in diameter. Irregularly shaped acicular crystals in spherulites are around  $1.5\ \mu\text{m}$  in diameter.

*Myostracum*: Irregular simple prismatic structure consisting of vertically aligned acicular crystals (Fig. 214). The average width of these crystals is  $0.3\ \mu\text{m}$ .



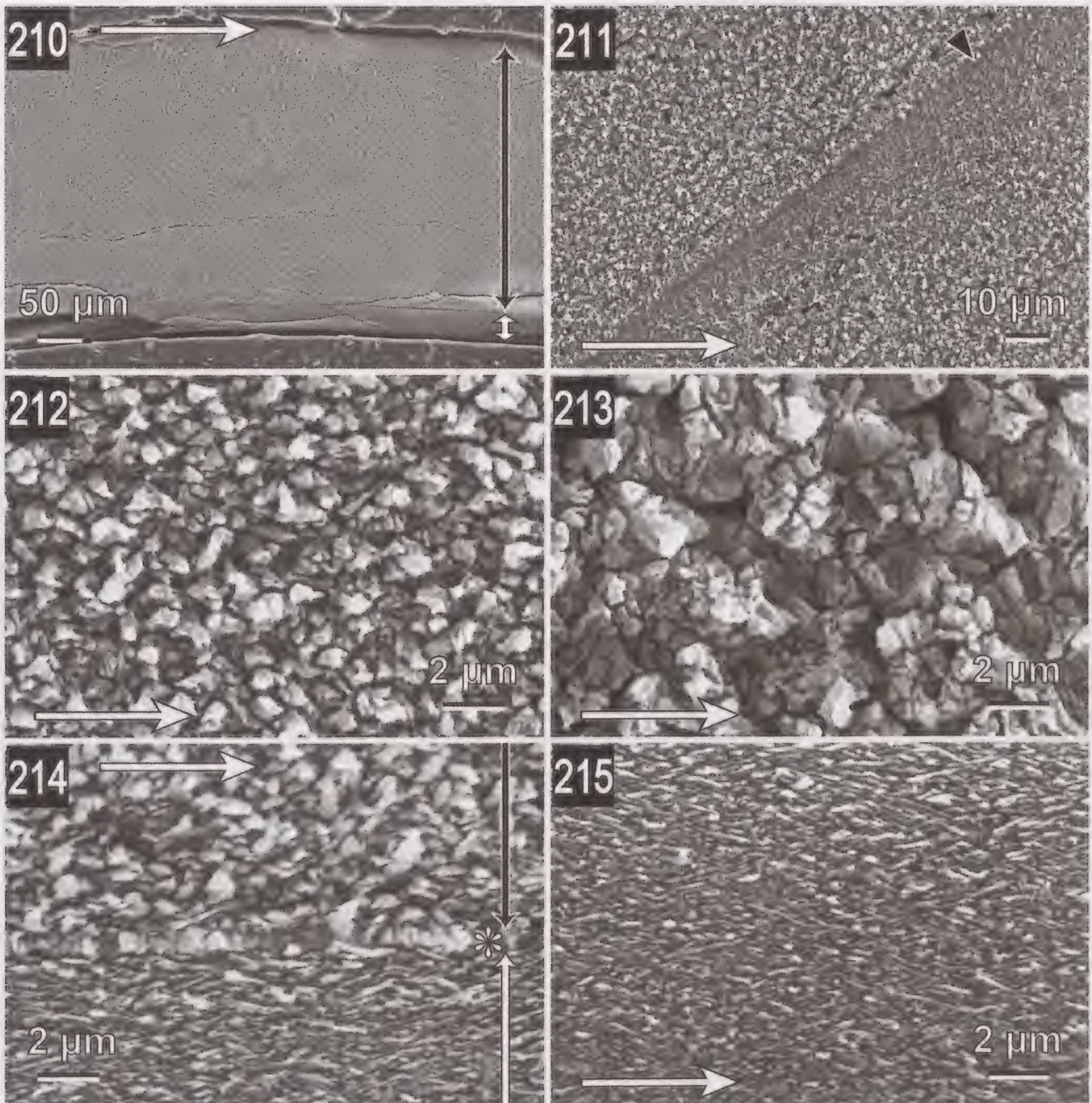
FIGS. 206–209. Scanning electron micrographs of *Tindaria soyoae* microstructure. Horizontal white arrow indicate growth direction. FIG. 206: Radial section of the outer and inner layers. Vertical black double-headed arrow, the outer layer; asterisk, the myostracum; white double-headed arrow, the inner layer; FIG. 207: Radial section of homogeneous structure of the outer layer; FIG. 208: Radial section of the outer, myostracum and inner layers. Vertical black double-headed arrow, the outer layer; asterisk, probable position of the myostracum; white double-headed arrow, the inner layer; FIG. 209: Radial section of homogeneous structure of the inner layer. FIGS. 206–209: Middle part of shell.



*Inner Layer:* Fine complex crossed lamellar structure (Figs. 214, 215). Acicular crystals composing the first-order lamellae of the fine complex crossed lamellar structure are around  $0.1\ \mu\text{m}$  wide and up to  $2.5\ \mu\text{m}$  long in the long axes and inclined at around  $25^\circ$  to the deposit surface.

*Megayoldia cf. japonica*  
(A. Adams & Reeve, 1850)  
(Figs. 28, 216–219)

*Shell Layers:* Outer, myostracum and inner layers are present. The outer layer thickens ven-



FIGS. 210–215. Scanning electron micrographs of *Megayoldia lischkei* microstructure. Horizontal white arrow indicate growth direction. FIG. 210: Radial section of the outer and inner layers. Vertical black double-headed arrow, the outer layer; white double-headed arrow, the inner layer; FIG. 211: Radial section of homogeneous and spherulitic structures of the outer layer; FIG. 212: Radial section of homogeneous structure of the outer layer; FIG. 213: Radial section of spherulitic structure of the outer layer; FIG. 214: Radial section of the outer, myostracum and inner layers. Vertical black double-headed arrow, the outer layer; asterisk, probable position of the myostracum; white double-headed arrow, the inner layer; FIG. 215: Radial section of fine complex crossed lamellar structure of the inner layer. FIGS. 210, 212, 214, 215: Middle part of shell; FIG. 211: Dorsal part of shell; FIG. 213: Ventral part of shell.



trally. The myostracum and inner layer thicken ventrally. The shell is up to approximately 400  $\mu\text{m}$  thick in the observed specimen.

**Outer Layer.** Fibrous prismatic and homogeneous structure (Figs. 216, 217). The outer sublayer of the outer layer consists of a fibrous prismatic structure (Fig. 216). The thickness of the outer sublayer is up to 16  $\mu\text{m}$ . Acicular crystals in the outer sublayer are up to 16  $\mu\text{m}$  long in the long axes, around 1.6  $\mu\text{m}$  in width, and recline at an angle of approximately  $65^\circ$  against the growth direction in a radial section. The long axes of the acicular crystals shorten inwards and become granular crystals in the homogeneous structure of the inner sublayer of the outer layer (Fig. 217). The average diameter of the granular crystals is around 0.6  $\mu\text{m}$ .

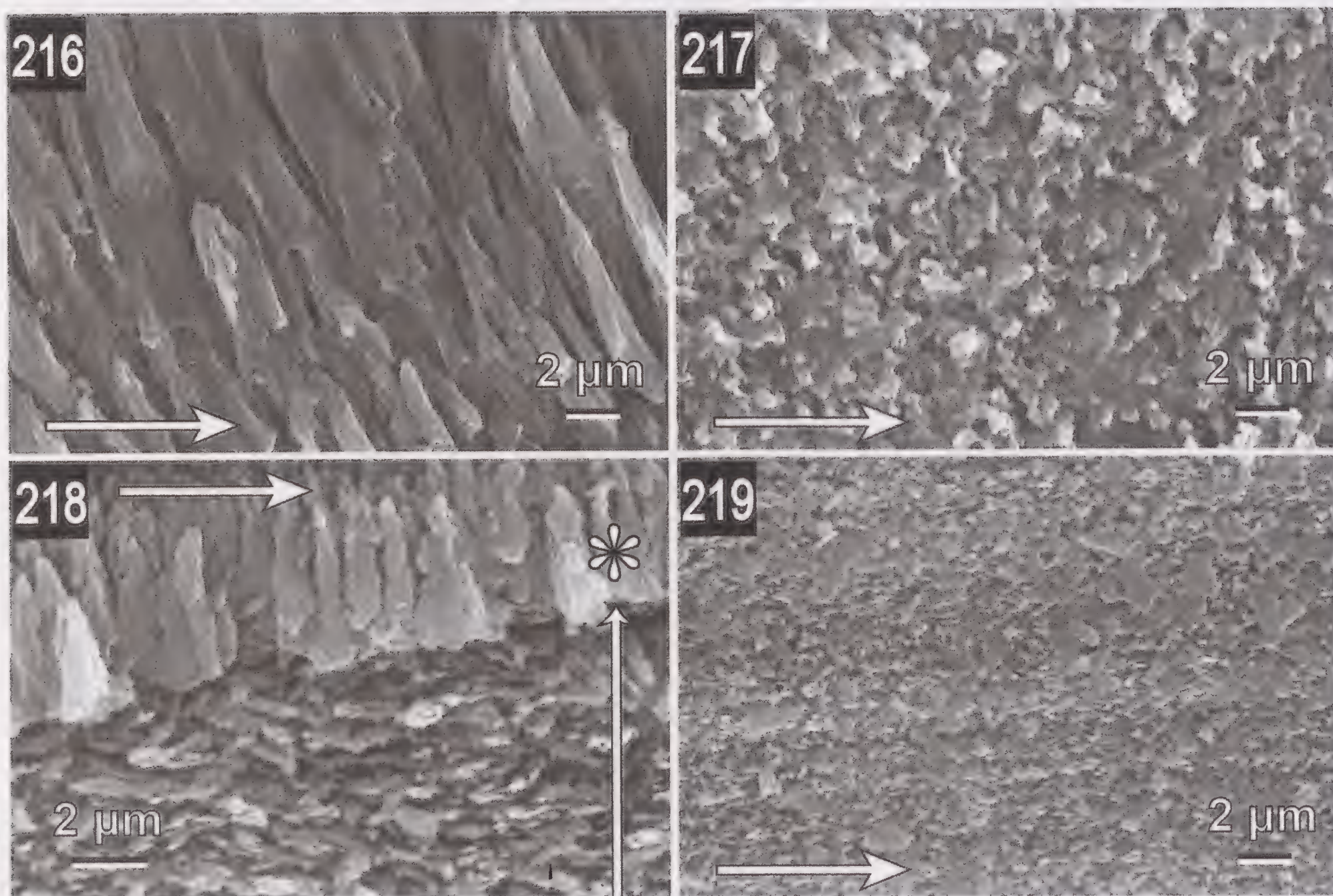
**Myostracum:** Obscure to irregular simple prismatic structure (Fig. 218). Vertically aligned acicular crystals in the irregular simple pris-

matic structure are around 0.8  $\mu\text{m}$  in width and up to 4  $\mu\text{m}$  long in the long axes. The thickness of the myostracum decreases ventrally and becomes obscure.

**Inner Layer.** Homogeneous or fine complex crossed lamellar structure (Figs. 218, 219). The diameter of granular crystals in the homogeneous structure are around 0.3  $\mu\text{m}$ . Acicular crystals composing the first-order lamellae of the fine complex crossed lamellar structure are around 0.3  $\mu\text{m}$  wide, up to 2  $\mu\text{m}$  long in the long axes, and inclined at around  $25^\circ$  degrees to the deposit surface.

*Yoldia seminuda* Dall, 1871  
(Figs. 29, 220–223)

**Shell Layers:** Outer, myostracum and inner layers are present (Figs. 220–223). The outer and inner layers thicken ventrally. The shell



FIGS. 216–219. Scanning electron micrographs of *Megayoldia* cf. *japonica* microstructure. Horizontal white arrow indicate growth direction. FIG. 216: Radial section of fibrous prismatic structure of the outer sublayer of the outer layer; FIG. 217: Radial section of homogeneous structure of the inner sublayer of the outer layer; FIG. 218: Radial section of the myostracum and inner layers. Asterisk, probable position of the myostracum; white double-headed arrow, the inner layer; FIG. 219: Radial section of homogeneous structure of the inner layer. FIGS. 216–219: Middle part of shell.



is up to approximately 420  $\mu\text{m}$  thick in the observed specimen.

*Outer Layer:* Homogeneous structure (Figs. 220, 221). Granular crystals comprising the homogeneous structure are variable in size, but around 0.6  $\mu\text{m}$  in diameter.

*Myostracum:* Irregular simple prismatic structure consisting of vertically aligned acicular crystals (Fig. 221). The average width and length of these crystals are 0.5  $\mu\text{m}$  and up to 4  $\mu\text{m}$  long in the long axes, respectively.

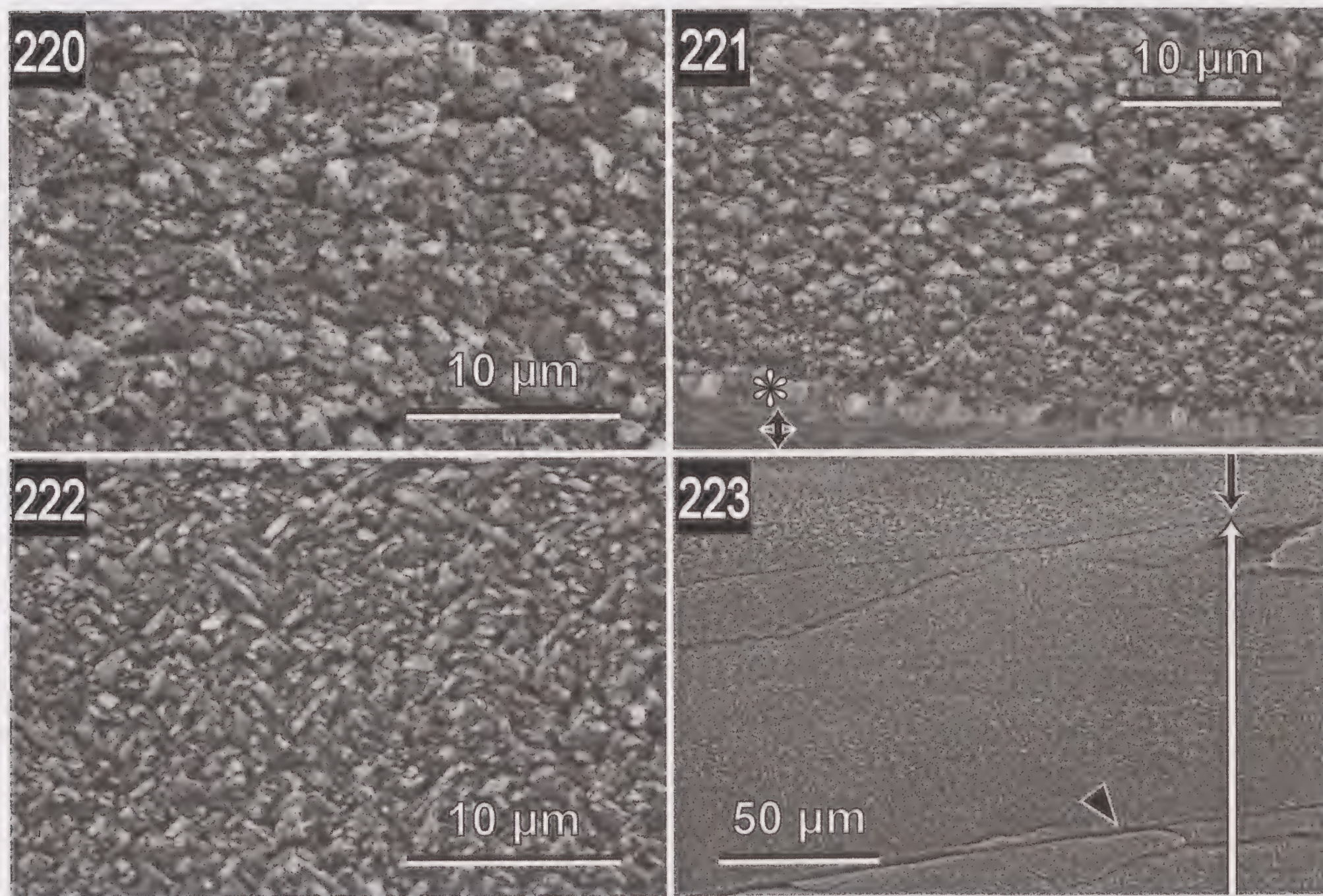
*Inner Layer:* Fine complex crossed lamellar structure (Fig. 222). Acicular crystals composing the first-order lamellae of the fine complex crossed lamellar structure are around 0.4  $\mu\text{m}$  in width and up to 4  $\mu\text{m}$  in length and inclined at around 30° to the deposit surface. Several growth lines composed of an irregular simple prismatic structure are present (Fig. 223).

*Yoldia notabilis* Yokoyama, 1922  
(Figs. 30, 224–229)

*Shell Layers:* Outer, myostracum and inner layers are present (Fig. 224). The outer and the inner layers thicken ventrally. In the outer layer, the growth lines are recognized as uniquely waved lines in a radial section along the oblique radial ribs and are well developed in a cyclic manner in the inner layer. The shell is up to approximately 360  $\mu\text{m}$  thick in the observed specimen.

*Outer Layer:* Homogeneous structure (Figs. 225, 226). Granular crystals in the homogeneous structure are variable in size but around 0.6  $\mu\text{m}$  in diameter.

*Myostracum:* Obscure to irregular simple prismatic structure (Fig. 226). Irregular simple prismatic structure consists of vertically



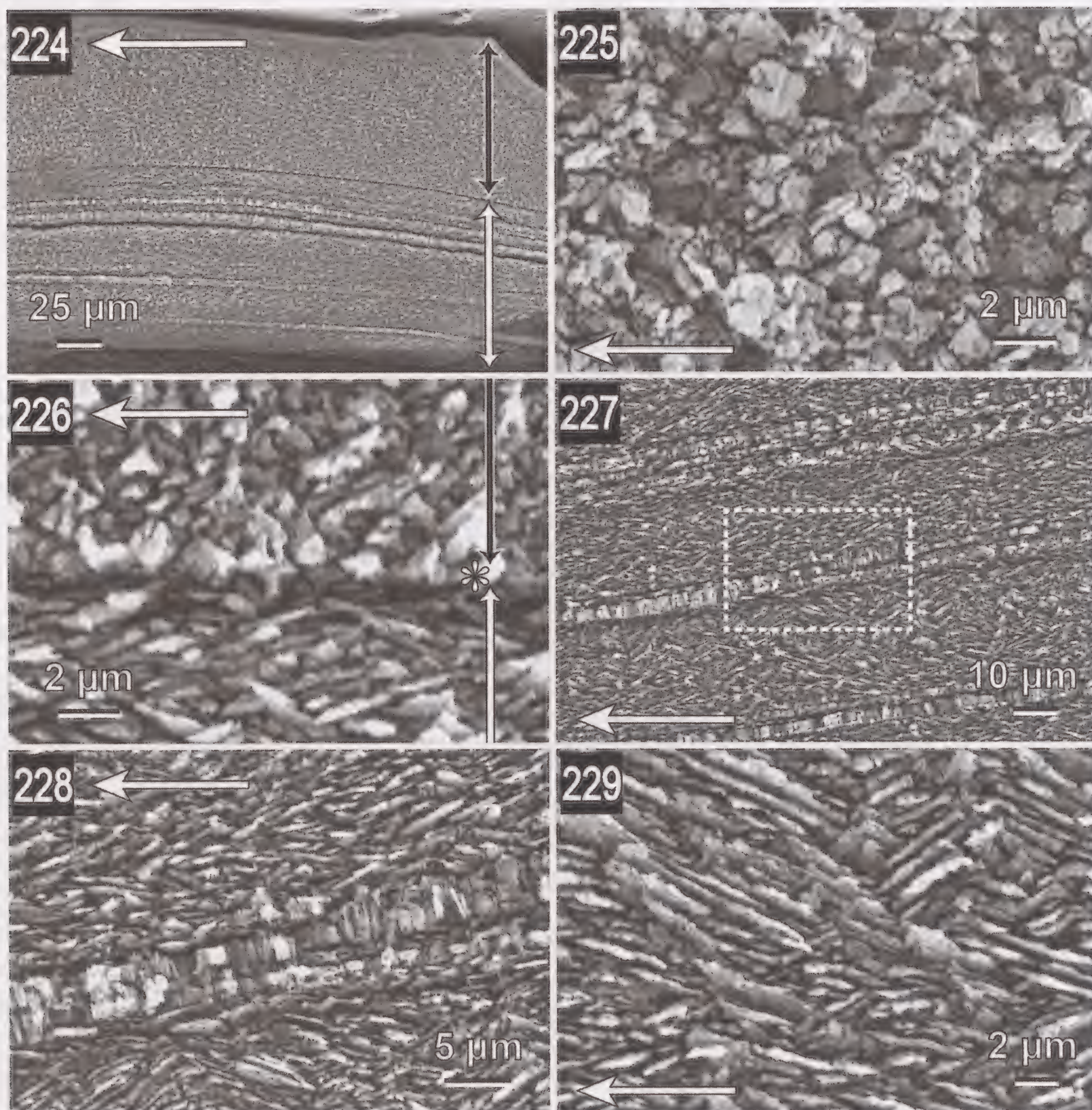
FIGS. 220–223. Scanning electron micrographs of *Yoldia seminuda* microstructure. Growth direction is left side in all figures. FIG. 220: Radial section of homogeneous structure of the outer layer; FIG. 221: Radial section of the outer and myostracum. Asterisk, the myostracum; black double-headed arrow, crack; FIG. 222: Radial section of fine complex crossed lamellar structure of the inner layer; FIG. 223: Radial section of the outer, myostracum and inner layers. Vertical black arrow, the outer layer; white double-headed arrow, the inner layer; black arrow head, growth line. FIGS. 220–222: Middle part of shell; FIG. 223: Dorsal part of shell.



aligned acicular crystals. The average width and length of these crystals are  $0.6\text{ }\mu\text{m}$  and up to  $0.7\text{ }\mu\text{m}$ , respectively.

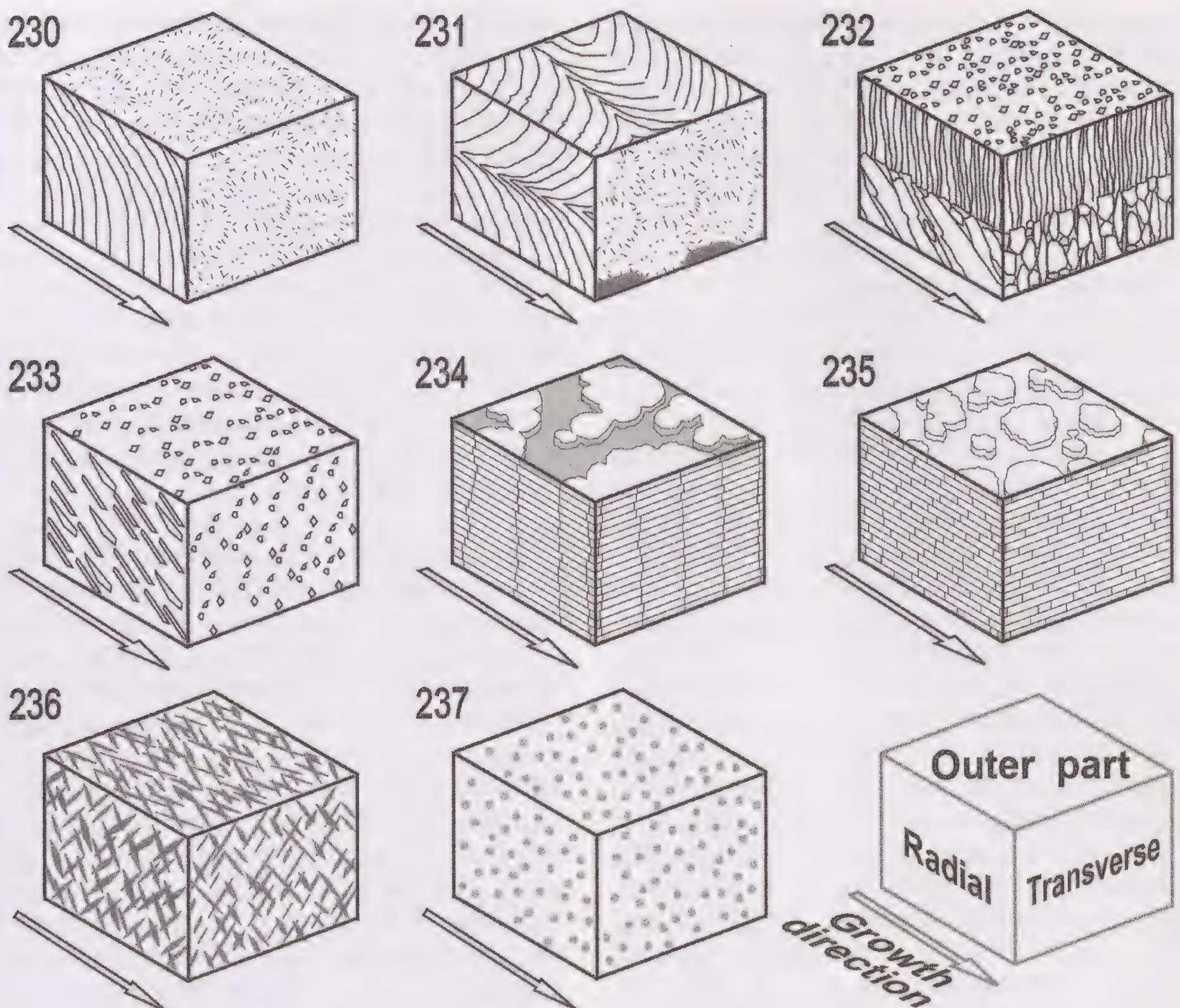
**Inner Layer.** Fine complex crossed lamellar structure (Figs. 226–229). Acicular crystals composing the first-order lamellae of the fine complex crossed lamellar structure are around  $0.3\text{ }\mu\text{m}$  wide, up to  $10\text{ }\mu\text{m}$  long in

the long axes, and inclined at around  $35^\circ$  to the deposit surface (i.e., inner surface of the shell). Growth lines are distributed periodically, and are composed of an irregular simple prismatic structure (Figs. 227, 228). Acicular crystals are vertically aligned and around  $1\text{ }\mu\text{m}$  in width and  $4\text{ }\mu\text{m}$  long in the long axes.



FIGS. 224–229. Scanning electron micrographs of *Yoldia notabilis* microstructure. Growth direction is left side in all figures; FIG. 224: Radial section of the outer and inner layers. Vertical black double-headed arrow, the outer layer; white double-headed arrow, the inner layer; FIG. 225: Radial section of homogeneous structure of the outer layer; FIG. 226: Radial section of the outer, myostracum and inner layers. Vertical black arrow, the outer layer; asterisk, the myostracum; white double-headed arrow, the inner layer; FIG. 227: Radial section of fine complex crossed lamellar structure of the inner layer. Several growth lines was observed; FIG. 228: Closer view of broken-lined square in Fig. 227; FIG. 229: Closer view of radial section of inner fine complex crossed lamellar structure. FIGS. 224–226: Middle part of shell; FIGS. 227–229: Dorsal part of shell.





FIGS. 230–237. Schematic representation of the shell microstructures in Nuculoidea, Manzanelloidea and Nuculanoidea. White arrow indicates growth direction. FIG. 230: Composite prismatic structure; FIG. 231: Denticular composite prismatic structure; FIG. 232: Irregular fibrous prismatic structure; FIG. 233: Fibrous prismatic structure; FIG. 234: Columnar nacreous structure; FIG. 235: Sheet nacreous structure; FIG. 236: fCCL structure; FIG. 237: Homogeneous structure.

## DISCUSSION

### Characteristics of Protobranch Shell Microstructure

Observations of shell microstructure in this and previous studies revealed several similar patterns of layer distribution and crystal morphology among protobranch superfamilies as summarized below (see also Sato et al., 2013, for Solemyoidea).

**Nuculoidea:** It has been acknowledged that the shell microstructure of Recent Nuculidae is characterized by having outer prismatic and middle/inner nacreous structures (e.g., Bøggild, 1930; Van de Poel, 1955; Taylor et al., 1969; Speden, 1970; Carter, 1990a). In this study,

prism-nacreous condition was confirmed in all observed species in Nuculidae.

Three types of prismatic structures, that is, composite prismatic, denticular composite prismatic and fibrous prismatic structures, has been documented in the outer layer of Recent nculids by previous studies (e.g., Carter, 1990a). Our detailed observations detected notable variations of these three prismatic structures. We redefined them into seven types: (1) irregular spherulitic prismatic structure (ISphP), (2) nondenticular composite prismatic structure (NDCP), (3) irregular nondenticular composite prismatic structure (INDCP, new name), (4) denticular prismatic structure, (5) irregular fibrous prismatic structure (IFP) of Carter et al. (2012), (6) irregular fibrous prismatic structure type-A (IFP type-A, new name),



(7) irregular fibrous prismatic structure type-B (IFP type-B, new name) (Table 2). The type of the prismatic structure are not common among three *Acila* species; INDCP in *A. mirabilis*, IShpP in *A. minutoides* and IFP with IShpP in *A. insignis*. Three distinct prismatic microstructures were observed among *Ennucula* species: (1) *Ennucula* sp. 2 has the IShpP, as is found in *Acila* species. (2) *Ennucula tenuis* and *E. niponica* have the NDCP. (3) The outer layers of *E. siberutensis* and *E. sp.1* are composed of the IFP type-B. *Brevinucula* sp. has the IFP type-A. Two *Nucula* species, *N. sp.* and *N. gemmulata*, have the denticular composite prismatic structure.

In Nuculoidea, the shell microstructure of the outer layer seems to provide crucial signals for their higher systematics in addition to the presence or absence of shell sculptures and crenulate inner ventral margin as in traditional classifications (e.g., Coan & Valentich-Scott, 2012). Based on shell microstructural characters, the validity of the genus *Ennucula* is questionable, since the shell microstructure of the outer layer is not common among *Ennucula* species. One of conventional diagnostic characters of *Ennucula* is non-crenulated inner ventral margin (Maxwell, 1988; Kilburn, 1999). However, Coan et al. (2000) pointed out the possibility that the smooth margins (i.e., non-crenulated inner ventral margin) in Nuculoidea can actually have microscopic crenulations. In addition, Sharma et al. (2013) suggested the absence of ventral crenulations is symplesiomorphy within nukulids based on their molecular phylogenetic analysis. *Ennucula* sp. 2 in this study might be genetically far from other *Ennucula* species, because its outer layer is composed of composite prismatic structure type-A which was also observed in *Acila* species.

Sheet nacreous structure was observed in the inner layers of all examined nukulids. However, occurrence of columnar or sheet nacreous structure in the middle layer was irregularly found among various species. No clear relationship was found among taxonomy, environment factors and occurrence of columnar nacreous structure. Body size could be a possible factor, since columnar tablet stacking had not been known in smaller specimens. Towered growth of the columnar nacreous structure is probably a strategy to thicken the shell rapidly (Wise, 1970; Checa et al., 2006). This hypothesis seems reasonable to explain the occurrence of columnar nacreous structure

in large-sized nukulids. Another possibility is difficulty in observation. Columnar nacreous structures of nukulids gradually shift to sheet nacreous structure towards the shell interior in the middle layer. Thus, columnar stacking of nacre tablets are hardly traceable in small nukulid specimens due to their thinness.

Occurrence of the myostracum was not verified in some species. The myostracum is normally found at molluscan shell interior where the adductor and pallial muscles attach (e.g., Taylor et al., 1969). However, the myostracum becomes thinner toward ventral part in most species and almost disappears (Figs. 41, 42, 76, 77, 86 and 87).

**Manzanelloidea:** We observed the shell microstructure of one species of Manzanelloidea, *Huxleyia sulcata*. Its shell is mostly composed of homogeneous structure. The other genus of Manzanelloidea, *Nucinella* have irregular simple prismatic to nearly homogeneous structure in the outer layer, fine CCL to homogeneous structure in the middle layer, and fine/irregular CCL structure in the inner layer (Carter, 1990a). Manzanelloidea are considered as a sister group of Solemyoidea due to their anatomical features (Allen & Sanders, 1969). The monophyly of the order Solemyoidea, which contains Solemyoidea and Manzanelloidea, was also supported by molecular phylogenetic analysis in Bieler et al. (2014). In spite of their anatomical and phylogenetic closeness, the shell microstructure of Manzanelloidea and Solemyoidea are completely different. Recent solemyids have a unique shell microstructure in their outer layer, that is, radially elongate simple prismatic (RESP) or reticulate structure (Sato et al., 2013). Sato et al. (2013) showed that shell microstructures in solemyids are more diversified than previously perceived. In addition, the shell microstructural composition of the two genera of Manzanelloidea, *Nucinella* (Carter, 1990a) and *Huxleyia* (this study) was different. These differences in shell microstructure are interpreted to be autapomorphic.

**Nuculanoidea:** Multiple polyphyletic conditions were revealed in interfamilial relationships of Nuculanoidea (Sharma et al., 2013), and therefore interpretation is not straightforward regarding character state distribution and their evolutionary pathways in this superfamily. However, species of Nuculanoidea observed in this study share homogeneous or fine CCL structures. These microstructures seem to be



possible synapomorphies of this taxon. Furthermore, the crystal size of nuculanids commonly diminish inwardly except for *Yoldia notabilis* and two *Malletia* species, which have complex crossed lamellar structure with well-developed acicular crystals in their inner layer. Sharma et al. (2013) suggested the systematic position of the family Sareptidae should be revised from Nuculoidea to Nuculanoidea based on their result of molecular analysis. Intriguingly, two sareptids share identical shell microstructural characteristics with nukulanoideans.

In addition to above examples, shell microstructural composition seem to be meaningful for genus-level systematics in the following two cases: (1) Three *Neilonella* species have similar shell microstructural composition, that is, outer fibrous prismatic and middle/inner homogeneous structures. (2) Two *Yoldia* species and two *Malletia* species commonly have outer homogeneous and inner fine complex crossed lamellar structures.

On the other hand, part of shell microstructural composition may not be stable criteria for genus-level systematics. For example, the outer layer of five *Nuculana* and two *Megayoldia* species show interspecific variations. Fibrous prismatic structure is found in *Nuculana tanseimaruae*, *N. gordonis* and *M. cf. japonica*, but not in *N. cf. soyoae*, *N. leonina*, *N. yokoyamai* and *M. lischkei*. Therefore, the fibrous prismatic structure might have no phylogenetic significance, or polyphyly of these species might cause this situation. Further study is required on molecular phylogeny of Nuculanoidea for this topic.

#### Comparison with Other Molluscan Higher Taxa in Shell Microstructure

**Prismatic Structure:** The shell consisting of the outer prismatic and inner nacreous structures is widely recognized in Recent bivalves (Mytiloidea and Pterioidea in Pteriomorpha, Palaeoheterodonta, and most Anomalodesmata except Cuspidarioidea, and some species of Poromyoidea and Thracioidea: Taylor et al., 1973; Carter, 1990a; Harper et al., 2000; Génio et al., 2012). However, the typical form of nukulid prismatic structure is not common in other molluscan taxa. (1) The simple prismatic structure in Pterioidea, Palaeoheterodonta and some Anomalodesmata differs from the prismatic structures in nukulids in having moderate length/width ratios. (2) The simple prismatic structure of Palaeoheterodonta and Anomal-

odesmata consists of aragonite, although that of Pterioidea is calcitic. (3) Some nukulids have thin fibrous prismatic structure in their outer layer, and a similar structure is also found in Mytilidae. But their mineral composition is aragonitic in protobranchs and calcitic in Mytilidae.

**Nacreous Structure:** Nacre appears in four of eight molluscan classes (Gastropoda, Bivalvia, Cephalopoda and Monoplacophora) (Checa et al., 2009b; Frýda et al., 2010). Although various types of aragonitic laminar structure are collectively called nacre or nacreous structure, the arrangement patterns of nacreous tablets differ from each other among molluscan subgroups. Nacre tablets stack in terraced arrangement in the most cases of Bivalvia, but in towers in Gastropoda (Wada, 1966; Cartwright & Checa, 2007; Checa et al., 2009a). In cephalopods, nacre shows a mixed structure with towered and terraced growth (Mitchel & Phahey, 1995). Previous microstructural studies have often defined nacre as sheet nacreous structure in bivalves and as columnar nacreous structure in gastropods and cephalopods (e.g., Taylor et al., 1969; Carter, 1990a, b). However, this generalization needs more detailed discussion as made below.

- (1) Columnar nacreous structure in Bivalvia: vertically stacked nacre tablets were exceptionally observed in the middle layers of some species of Mytilidae (subclass Pteriomorpha), Unionoidea and Trigonioidea (both subclass Palaeoheterodonta) and Nuculidae (subclass Protobranchia) (Taylor et al., 1969; Carter, 1990a; Frýda et al., 2010; Génio et al., 2012). This vertically stacked nacre in bivalves have been defined as columnar nacreous structure identical to that of gastropods and cephalopods by Carter (1990a). Taylor et al. (1969) have called them "lenticular nacreous" structure but this terminology was not adopted by authors after Carter (1990a).
- (2) Spiral growth of tablets: in this study, we recognized the spiral growth of nacre tablets in *Acila mirabilis* both in columnar nacre (Fig. 38) and sheet nacre (Fig. 40). Therefore, these two nacreous layers in the middle and inner shell layers of Nuculidae are probably regarded as the products created by the same mechanism of crystal growth. Compared with that of gastropods, vertical nacre stacking in Nuculidae seems not to be controlled by a strict law. Yao et al. (2006, 2009) also showed spiral growth of nacre



tablets in gastropod *Haliotis rufescens*. Thus, bivalves and gastropods possibly share a similar mechanism for crystal growth of nacre tablets. Sheet nacreous structure, however, have never been recognized in gastropods.

- (3) Transition from columnar to sheet nacreous structures: columnar nacreous structure of protobranches gradually shift into sheet nacreous structure towards the shell interior in the middle layer of nuchids. This is also recognized in the nacreous layer of *Nautilus pompilius* which changes configuration patterns of nacre tablets inwardly from tower-like to terrace-like stacking like the middle-inner nacre of bivalves (Checa et al., 2009b).
- (4) Origin and differentiation of molluscan nacre: Vendrasco et al. (2011) hypothesized that nacre of each molluscan class (Gastropoda, Bivalvia and Cephalopoda) has independent origins based on fossil records. While nacreous structure has been traditionally thought to be a primitive shell microstructure among Conchifera, nacre-bearing molluscs from the Cambrian have not been found. Instead of nacre, foliated (or semi-foliated) aragonite was confirmed to occur in the shells of the Cambrian molluscs and many Recent monoplacophorans, which are considered as the most primitive taxa of Conchifera. Thus, above-mentioned differences of nacreous structure among different classes indicate that various types of nacre are probably due to their convergent evolution.

**Homogeneous Structure:** This structure is dominant in the shell of Nuculanoidea. Homogeneous structure is also found in *Huxleyia sulcata* shell (this study) and the inner layer of *Solemya pusilla* (Sato et al., 2013), which are both belong to Solemyoidea. Other solemyids have different shell microstructure (e.g., radially elongate simple prismatic and reticulate structures) in corresponding shell layers, but similarly granular crystals constitute the second- or third-order units of these microstructures. Granular crystals are main constituents of homogeneous and related structures of protobranches.

A thin layer of homogeneous structure is found between the periostracum and outer layer in some Mytilidae, but it is calcitic (Génio et al., 2012). Several groups of Heterodonta also have the homogeneous structure similar to that of Nuculanoidea (Taylor et al., 1973). Crossed lamellar and/or complex crossed lamellar structures seem to be equivalent to homogeneous structure in Heterodonta, since these structures

co-exist within the same shell layers of same genera or species. On the other hand, fibrous prismatic and fine CCL structures co-occur with homogeneous structure in Nuculanoidea. Accordingly, homology of homogeneous structure needs further reconsideration.

Shimamoto (1986) examined inter- and intraspecific differences of the shell microstructure of Veneridae and found that the homogeneous structure prevail in infaunal species. He mentioned that crossed lamellar structure is replaced with homogeneous structure in connection with adaptations for burrowing habits. However, no such a relationship was found between the occurrence of shell microstructure and the habitat (e.g., water depth) in Nuculanoidea.

### Systematic and Paleontological Implications

Our observations suggest that the shell microstructure of Recent protobranches is highly conservative at least at a superfamily level. However, this is doubtful from paleontological evidence. There are several studies reporting (1) nacre-bearing nuchanids (Taylor et al., 1969; Speden, 1970; Carter, 1990a) and (2) nacre-lacking nuchids (Bøggild, 1930; Carter, 1990a) from the Paleozoic and Mesozoic, contradicting to generalization in Recent forms. This is also true for the shell microstructure of Solemyidae. Nacre-bearing solemyids were reported from the Carboniferous (Carter, 1990a), but nacreous structure has never been known in Recent species (Sato et al., 2013).

Shell microstructure of Fordillidae, ancestral bivalves from the Cambrian, is semi-foliated aragonite, which is considered as a primitive nacreous structure (Vendrasco et al., 2011; Carter et al., 2012). The oldest nuchloidean and nuchlanoidean fossils with shell microstructural data possessed laminar shell microstructure, which is probably primitive nacre (Vendrasco et al., 2013). These data suggest nacreous structure as is found in the Paleozoic fossils is one of the ancestral states of the shell microstructure of protobranches, and the shell microstructure composition found in Recent protobranches may be a secondary condition derived from the primitive laminar shell microstructure.

For future research, we need more microstructural data across entire groups of protobranches. Unusual shell microstructures which were not observed in the present study have been reported in several Recent species in the past. (1) Carter (1990a) showed that certain specimens of *Nucula proxima* have a small patch of fine CCL or homogeneous structures immediately



below the umbo within the inner shell layer. (2) Carter (2001) also reported an ontogenetic change in *Condylonucula maya*. The species has fibrous to irregular prismatic structure in their outer layer, and the middle and inner layers consist of nacreous structure in a juvenile stage. Later in ontogeny, these two layers are differentiated into homogeneous and irregular simple prismatic structures, respectively. (3) Nacre-baring species were also reported in Recent nuculanids (*Silicula* sp. and *Phaseolus* sp.; Nevesskaya et al., 1971), although they did not show any image in their paper. The accuracy of their descriptions should be verified. These above-mentioned examples indicate the necessity of further observations along with a robust molecular phylogeny of Recent forms with better taxonomic coverage.

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## INVASION OF FRESHWATER MOLLUSCS IN THE CZECH REPUBLIC: TIME COURSE AND ENVIRONMENTAL PREDICTORS

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### ABSTRACT

The number of non-native species has dramatically increased over the last decades in many aquatic habitats of central Europe. Although the spreading of alien mollusc species can poses a serious threat to many native species, no attempt has been made to assemble and analyse an extensive dataset collected over a long time span. So far, eight non-native species of aquatic molluscs – five gastropods and three bivalves – have been recorded in the wild in the Czech Republic in central Europe. We assembled a dataset consisting of 1,783 sites with the presence of these non-native species recorded between 1891 and 2014. We aimed to explore the time course and spatial pattern of the invasions and to define some of the gross predictors of the occurrence of these species by categorizing their sites based on habitat type, elevation and distance from the nearest large river. We found that most of these species expressed affinities to non-natural standing waters and large rivers. The most invaded parts of the Czech Republic were large lowlands, especially the Elbe River basin. In contrast, hilly and mountain areas were notably less invaded as the number of records sharply decreased towards higher elevations for all studied species except *Gyraulus parvus*. The highest invasion rate was documented for *Physella acuta* and *Potamopyrgus antipodarum*, in contrast to two modern invaders (*Menetus dilatatus* and *Corbicula fluminea*) that had a much lower rate of colonisation. However, the other four species showing an intermediate rate of spreading were recorded for the first time both 70 years ago (*Dreissena polymorpha* and *Ferrissia fragilis*) and less than 20 years ago (*Gyraulus parvus* and *Sinanodonta woodiana*). Large rivers serve as the most important corridors for the spreading of non-native species, with a significant association between the number of non-native species recorded and the distance from the 8<sup>th</sup>- and 9<sup>th</sup>-order rivers.

Key words: aquatic molluscs, Czech Republic, current distribution, non-native species, spreading, habitat affinities.

### INTRODUCTION

The spread of non-native species has been one of the leading threats to aquatic ecosystems over the last few decades (e.g., Abramovitz, 1996). Most of the natural barriers for the species dispersal have been weakened by human activities (Leppäkoski et al., 1991), thus allowing a long distance range expansion of many non-native species. Some of them have been found responsible for the loss of biodiversity, causing irreversible changes in the ecosystems (Wilcove et al., 1998; Alonso & Castro-Díez, 2008). A high number of non-native species of high densities are commonly found in aquatic ecosystems, especially in ar-

eas with frequent waterway transport and also in brackish regions. The global movement of ballast water by ships is considered the most frequent vector for the transfer of non-native species (Carlton, 1992; Zaranko et al., 1997; Pancucci-Papadopoulou et al., 2005).

Freshwater molluscs are among important groups of non-native species (Meier-Brook, 2002) as they are readily transported by humans and often have significant impact on native molluscs and their ecosystems. They can change trophic relationships (Zaiko & Olenin, 2006: *Dreissena polymorpha* (Pallas, 1771); Phelps, 1994: *Corbicula fluminea* (O. F. Müller, 1774)) and character of the substrate (Bódis et al., 2014: *C. fluminea*; Benkő-Kiss,

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2012: *D. polymorpha*, *Sinanodonta woodiana* (Lea, 1834)). They can also substantially alter concentration of phytoplankton, zooplankton, and organic and inorganic particles by filtration (Sousa et al., 2008; Phelps, 1994: *C. fluminea*; Karatayev et al., 1997: *D. polymorpha*). Some non-native aquatic molluscs were found to affect large bivalves (Ricciardi et al., 1998; Karatayev et al., 2007; Reichard et al., 2012: *D. polymorpha*) by disrupting host-parasite relationships (Rashleigh, 1995; Rogers & Dimock, 2003: *S. woodiana*) or transmitting parasites (Gérard & Le Lannic, 2003: *Potamopyrgus antipodarum* (Gray, 1843)). Thus, they may also reduce or eliminate native mollusc fauna by competition (Cowie, 2001). Significant economic impact was documented for *C. fluminea* and *D. polymorpha* (Pimentel et al., 2000; Minchin, 2008; Sousa et al., 2008), which may occur in extremely dense populations. They clog pipes of hydro power plants, water pipes, irrigation systems and the other industrial facilities using water (Gollasch & Leppäkoski, 1999; Minchin et al., 2002; Birnbaum, 2006). The catastrophic influence of *D. polymorpha* has been documented especially in the Great Lakes region (e.g., Dermott et al., 2005).

In the wild in the Czech Republic, eight non-native freshwater mollusc species have been recorded so far: bivalves *Corbicula fluminea*, *Dreissena polymorpha* and *Sinanodonta woodiana*, and gastropods *Ferrissia fragilis* (Tryon, 1863), *Gyraulus parvus* (Say, 1817), *Menetus dilatatus* (Gould, 1841), *Physella acuta* (Draparnaud, 1805) and *Potamopyrgus antipodarum* (Beran, 2002, 2006a; Horsák et al., 2013). Except for *D. polymorpha*, all these species are of non-European origin, four of them being introduced from North America. Although many records of these species have been published, no attempt has been made to summarise and analyse all the existing data. The main objective of this study is to track the time course of the invasions of these eight species between the first record and 2014. We also aim to identify the most readily invaded habitat types and distribution pattern of the invasion along the gradient of elevation. As large lowland rivers commonly serve as migration corridors for many non-native aquatic species, we analysed the relationship between the number of these eight species recorded in mapping grid cells and the distance of these mapping cells from the nearest large river.

## MATERIALS AND METHODS

### Data Collection and Mapping of Species Occurrence

Data about the occurrence of non-native species in the Czech Republic originate in almost 78% from personal databases of Luboš Beran and Michal Horsák. Some additional data were provided by Jan Špaček (Elbe River catchment data) and by the administrations of the Elbe River, Morava River, Odra River and Vltava River catchments. Species records were assigned to the central European mapping grid-cell systems based on the site GPS coordinates. The records of the same species in flowing waters were merged if the distance between sites of these records was less than 1 km. Species population densities standardized by a 30-minute interval of the collecting were categorized at four-point scale in mapping cells: 1 – one to two records with a low density (i.e., under approximately 50 individuals); 2 – two records with a high density (i.e., over 50 individuals) or three to four records with a low density; 3 – three to four records with a high density or five to six records with a low density; 4 – five to six records with a high density and more than six records. For each target species, a set of maps for different time slices was constructed in the ArcGIS programme (ESRI, 2013). The records of each species were mapped in various and arbitrary chosen time slices for the optimal visualization of the time course of each species spreading.

### Site Categorization and Predictors

The study sites were classified into four coarse habitat-categories as: (1) the 8<sup>th</sup>- and 9<sup>th</sup>-order rivers according to the Strahler stream order system (hereafter named as FlowLarge); (2) all the other running waters (FlowSmall); (3) natural or semi-natural standing water bodies such as pools, river arms, oxbows etc. (StandNatural); and (4) all the other standing water bodies, especially water reservoirs, dams, fish ponds and water bodies created by mining such as quarries and sand pits (StandArtificial).

To explore and visualize distribution of the target species along the gradient of elevation, we determined elevation of the study sites using the Google Earth programme in conjunction with site coordinates measured with GPS. The variation among the altitudinal distribution of



the eight non-native species was expressed using boxplots. To explore the presumption that large lowland rivers can act as important migration corridors for non-native species, we categorized each mapping cell based on its distance from the 8<sup>th</sup>- and 9<sup>th</sup>-order rivers. We used the following grade-scale categorization: 1 – the mapping cells that contain the 8<sup>th</sup>- and 9<sup>th</sup>-order rivers; 2 – the cells adjacent to the 1<sup>st</sup> grade cells (i.e., sharing the same cell side or corner); 3 – the cells adjacent to the 2<sup>nd</sup> grade cells; etc. Spearman correlations were used to explore relationship between the number of non-native species recorded in each mapping cell and the categorized distance of the cells from the nearest large river. The pattern for each species was further visualized using frequency histograms.

## RESULTS

The final dataset included eight non-native species reported from 1,783 sites assigned into 299 mapping cells, representing 44% out of all 674 mapping cells across the Czech Republic (Fig. 1); and 59% out of 504 mapping cells

from which more than ten records of aquatic molluscs exist. These species combined were found in both running waters (1,004 sites; 56% of all sites) and standing water bodies (779 sites; 44%). The highest number of records was documented for artificial standing waters (StandArtificial: 598; 34%) and small running waters (FlowSmall: 744; 42%). Fewer records exist from large rivers (FlowLarge: 260; 15%) and still fewer from natural standing waters (StandNatural: 181; 10%). Most of the non-native species tended to occur in artificial standing waters and large rivers (Fig. 2), however individual species greatly differed in number of their records among the four types of water bodies (Fig. 3).

The most invaded part of the Czech Republic was the Elbe River basin and lowland stretches of its tributaries (Fig. 1). All the studied non-native species frequently occurred in these areas mostly in dense populations, except for *Sinanodonta woodiana* (Figs. 4–11). The second most invaded area of the Czech Republic was the Morava River basin. In contrast, hilly and mountain areas, that is, cross-border mountain ranges and the Bohemian-Moravian Highlands, were notably less invaded (Fig. 1). The number



FIG. 1. Distribution of eight non-native aquatic molluscs recorded between 1891 and 2014 in the Czech Republic. Small point, 1 species; intermediate point, 2–3 species; larger point, 4–5 species; square, 6–7 species per mapping cell. The dash line shows the historical border between Bohemia (western part) and Moravia (eastern part).



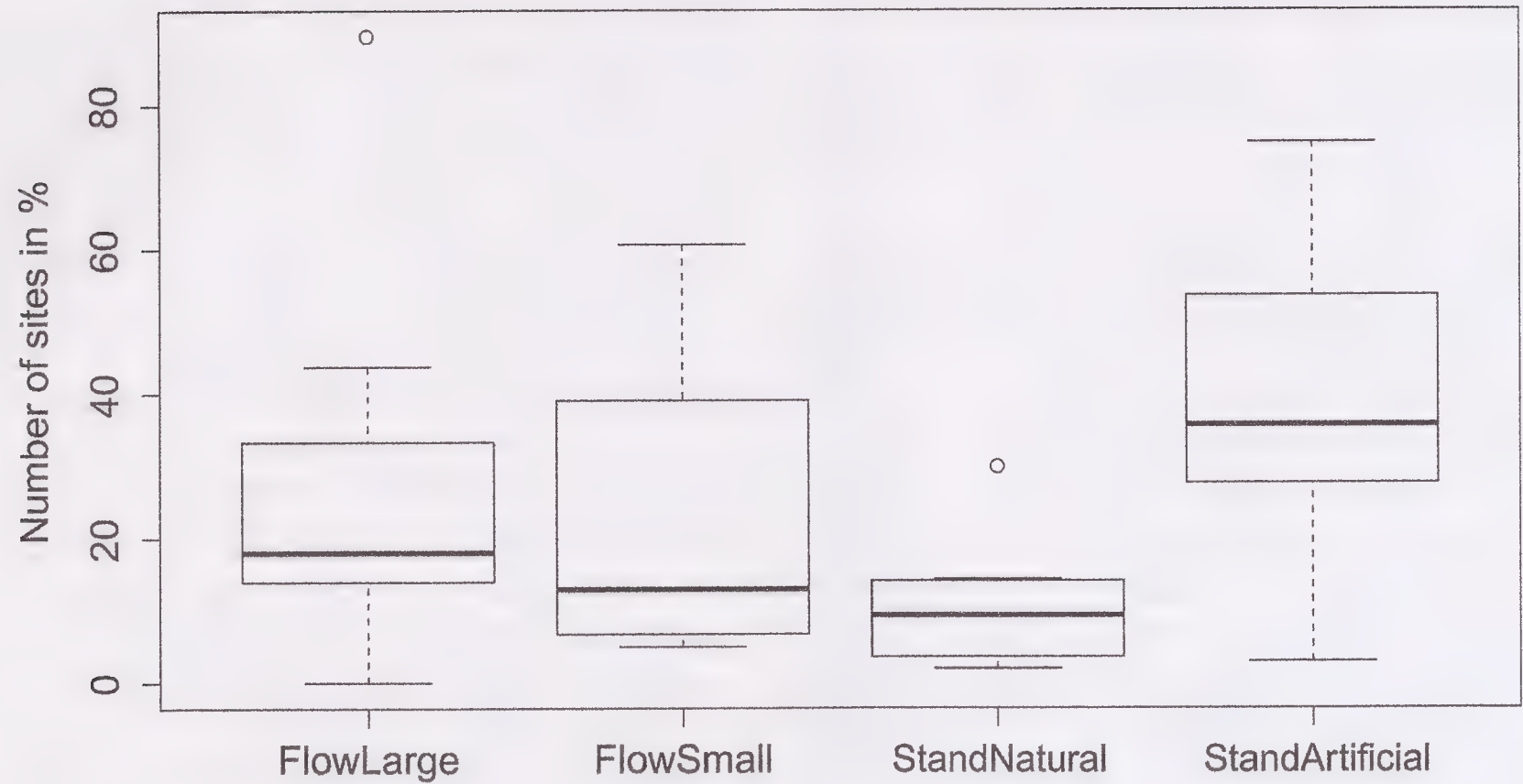


FIG. 2. Percentage representation of sites classified among four habitat types (for details see Methods) for each of eight non-native species. The central line of each box refers to the median value, box height to the interquartile range, whiskers to the non-outlier range (i.e., 1.5 times the interquartile range at each side), and small circles to outliers.

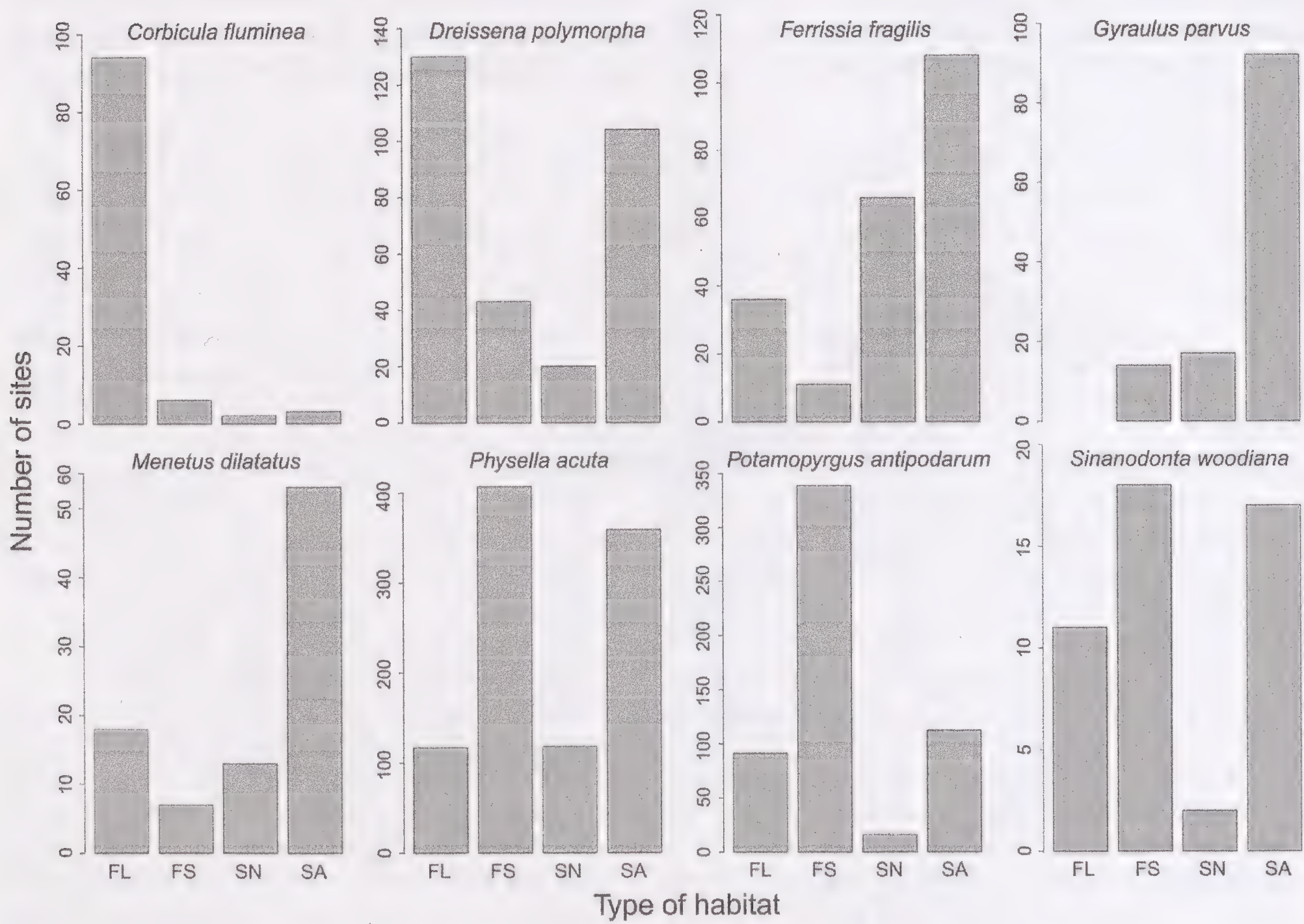


FIG. 3. Number of sites with the occurrence of the studied non-native species and classified among four habitat types: FL, FlowLarge; FS, FlowSmall; SN, StandNatural; SA, StandArtificial; for details see Methods. Note that the scaling of y-axes differs among species.



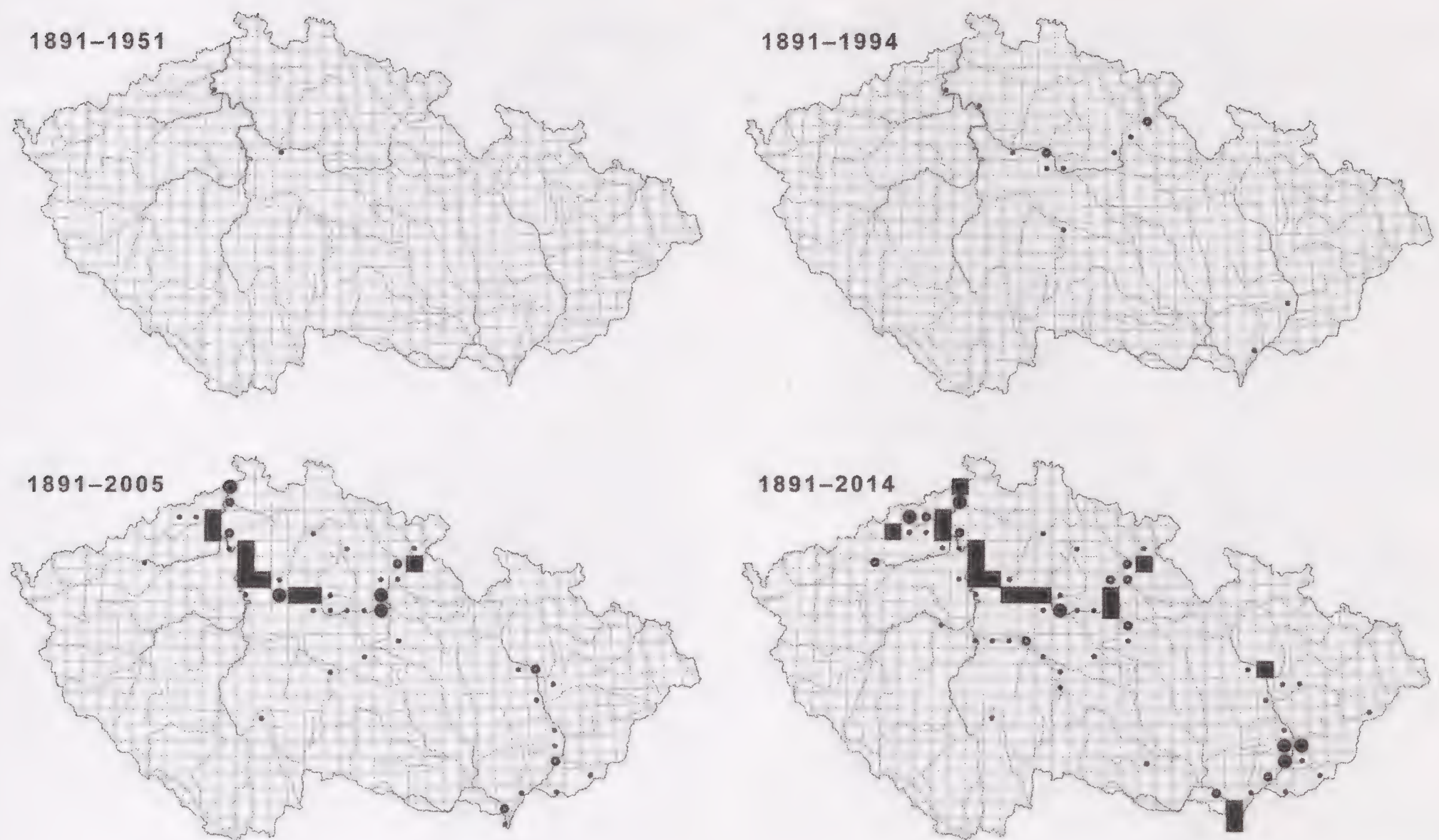


FIG. 4. Distribution of *Dreissena polymorpha* records in mapping cells of the Czech Republic plotted in four time intervals. Small point: 1–2 records with density under 50 individuals; intermediate point: 2 records with density over 50 individuals or 3–4 records with density under 50 individuals; larger point: 3–4 records with density over 50 individuals or 5–6 records with density under 50 individuals; square: 5–6 records with density over 50 individuals or 7 plus records.

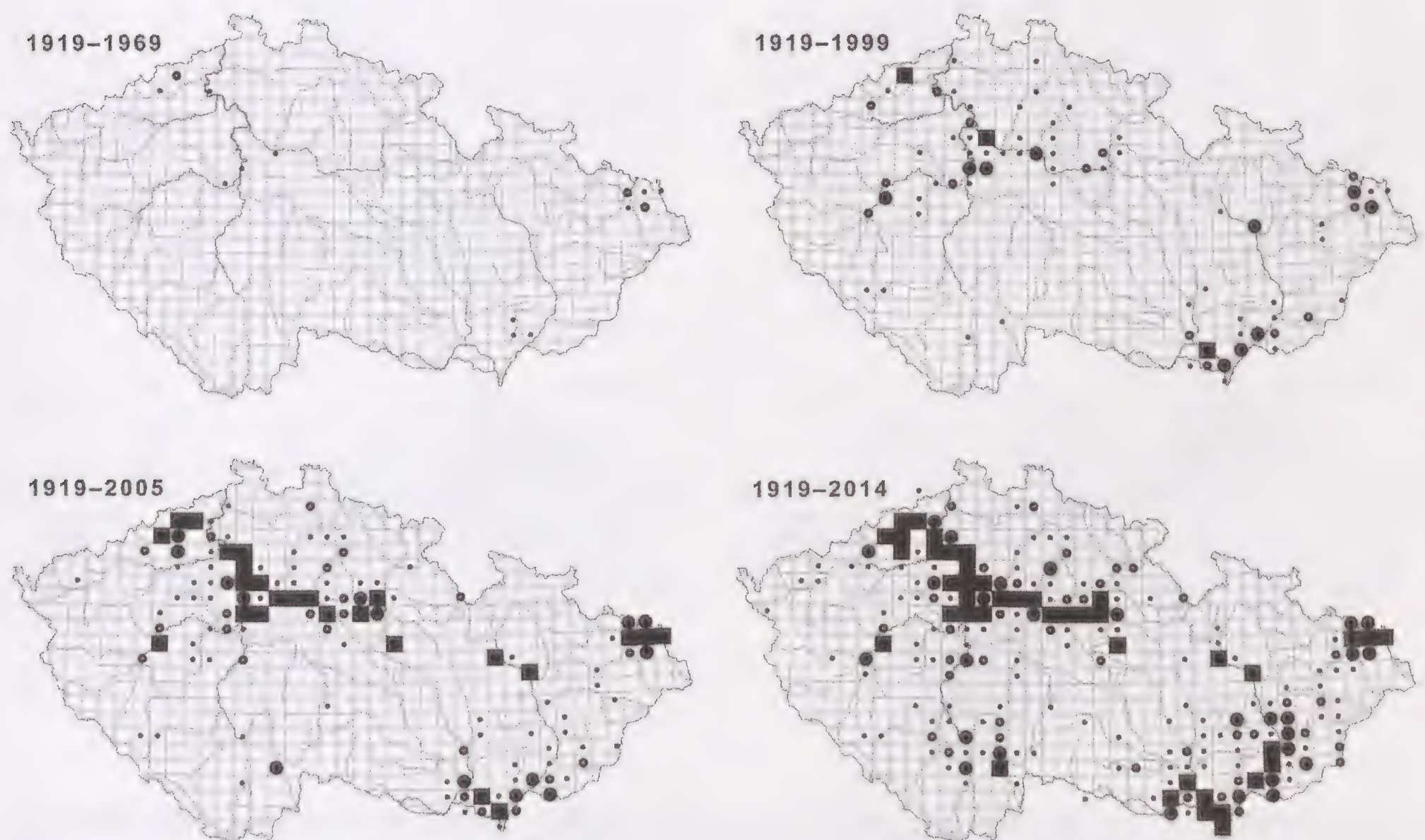


FIG. 5. Distribution of *Physella acuta* records in mapping cells of the Czech Republic plotted in four time intervals. For explanation of symbols, see Fig. 4.



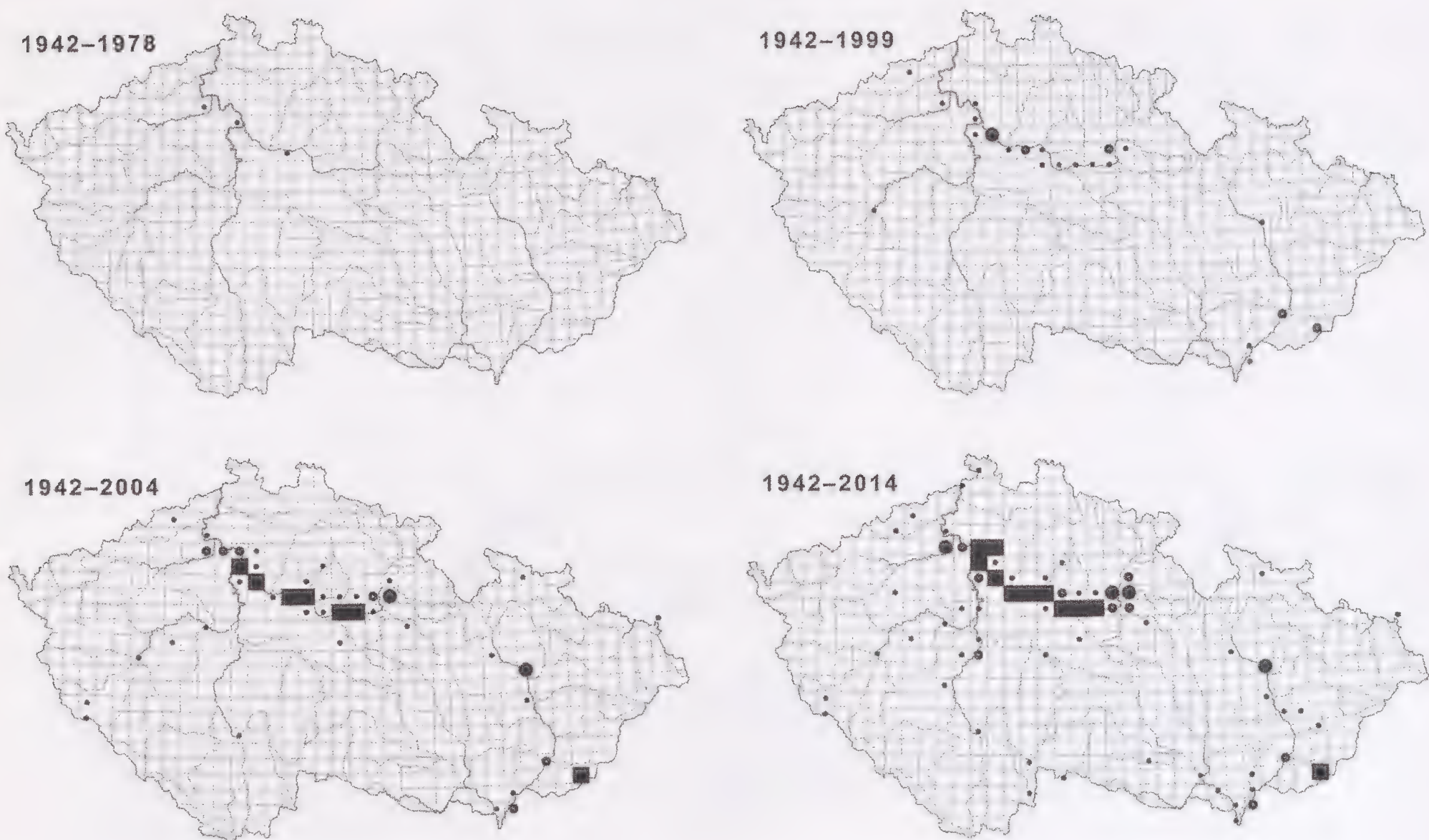


FIG. 6. Distribution of *Ferrissia fragilis* records in mapping cells of the Czech Republic plotted in four time intervals. For explanation of symbols, see Fig. 4.

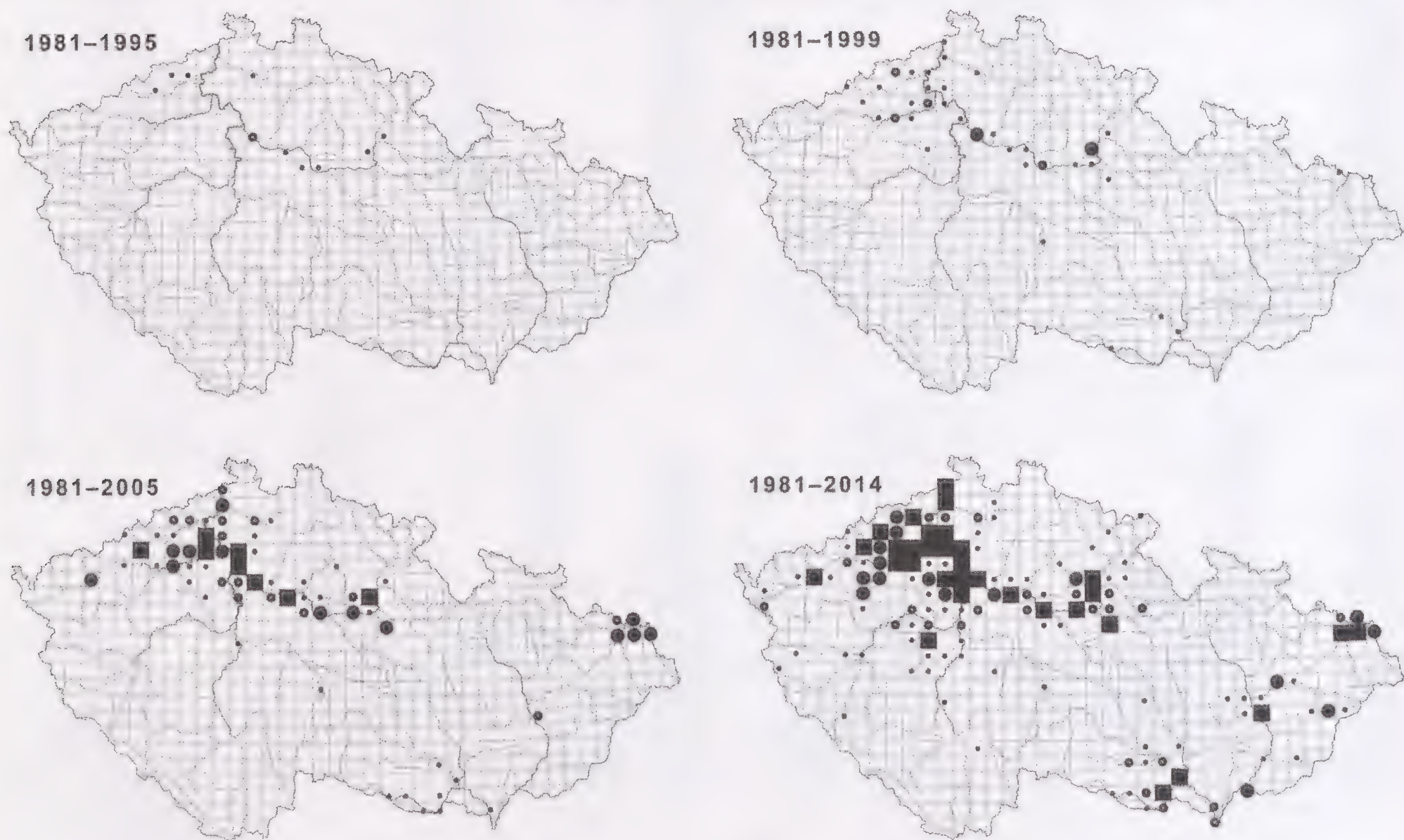


FIG. 7. Distribution of *Potamopyrgus antipodarum* records in mapping cells of the Czech Republic plotted in four time intervals. For explanation of symbols, see Fig. 4.



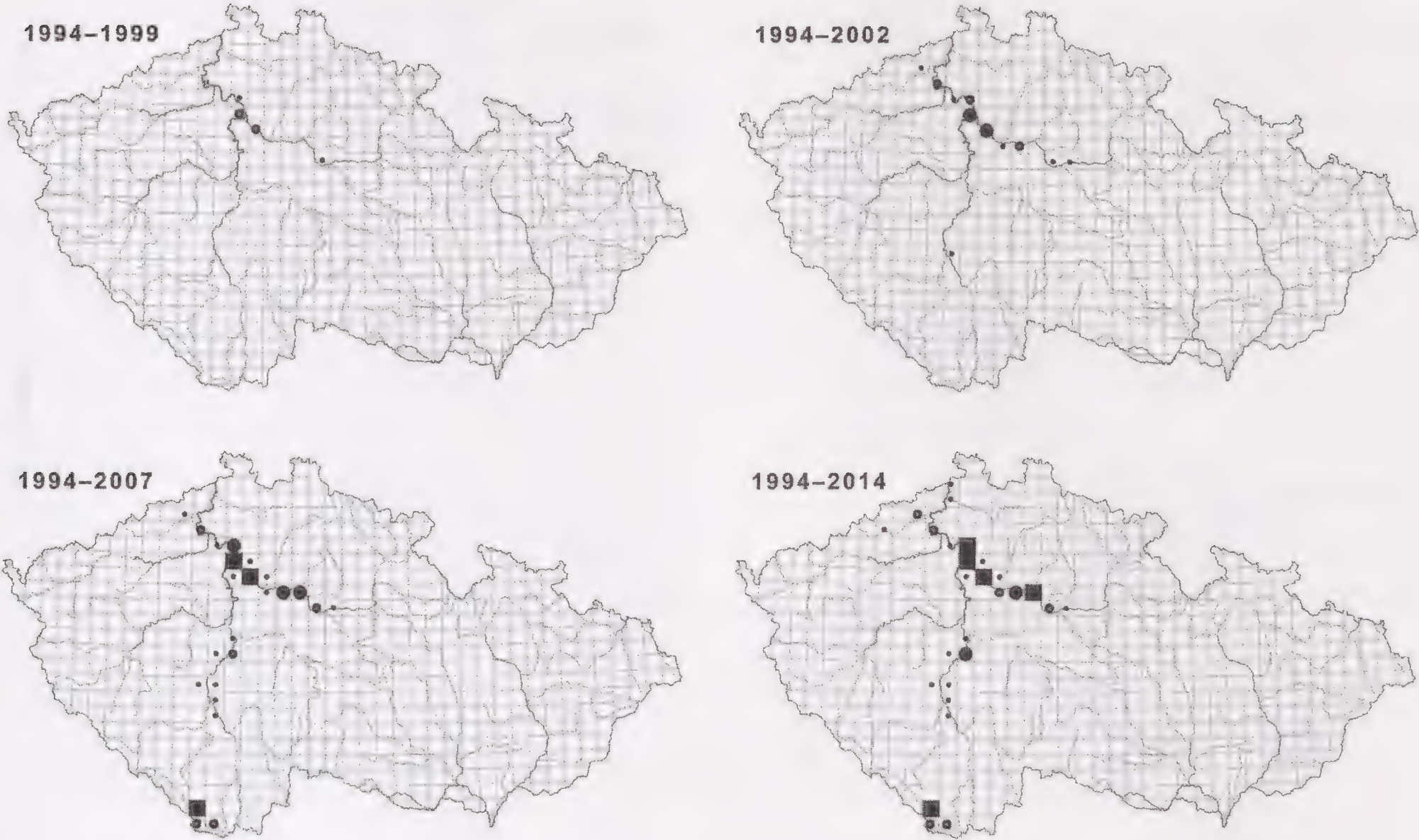


FIG. 8. Distribution of *Menetus dilatatus* records in mapping cells of the Czech Republic plotted in four time intervals. For explanation of symbols, see Fig. 4.

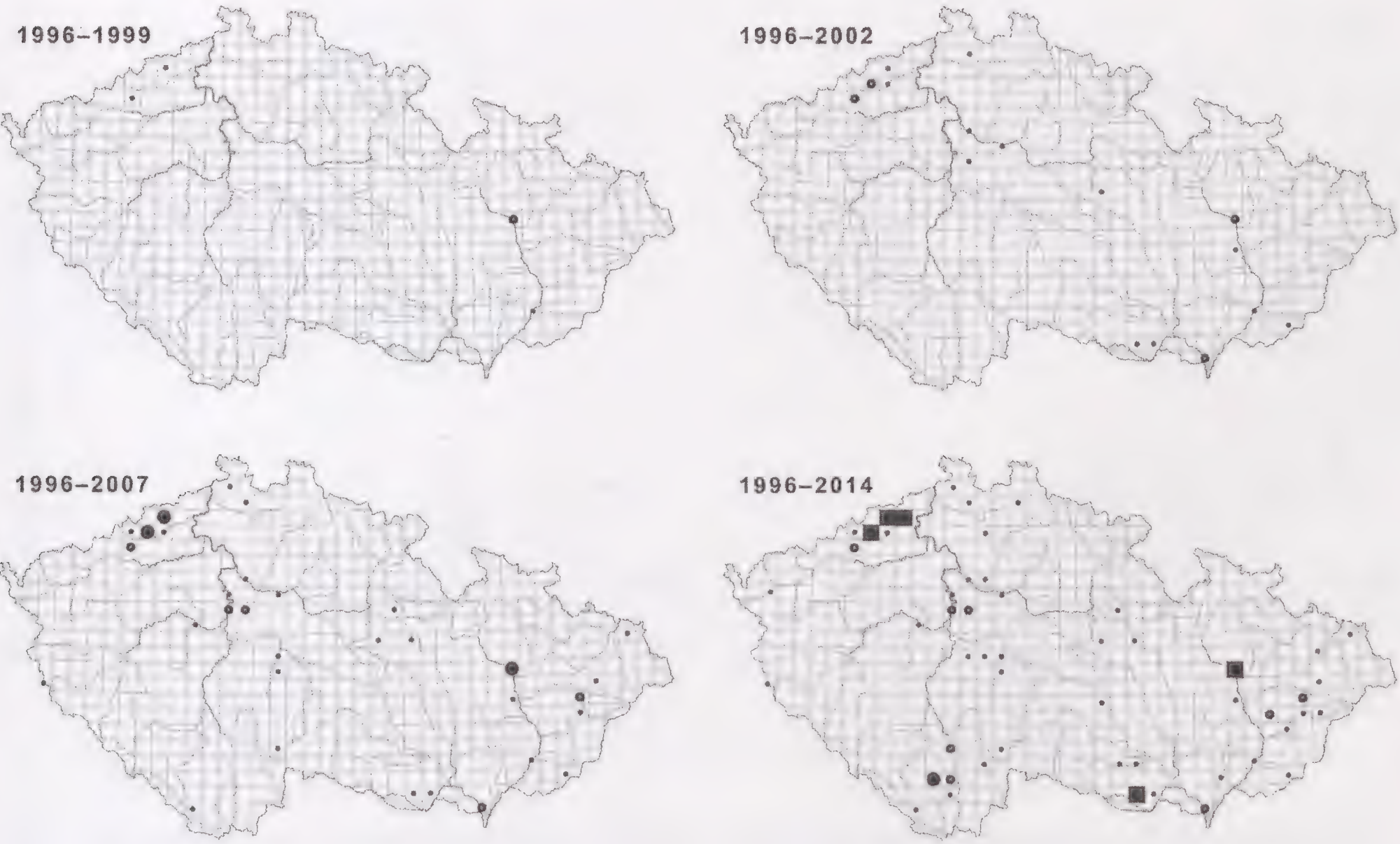


FIG. 9. Distribution of *Gyraulus parvus* records in mapping cells of the Czech Republic plotted in four time intervals. For explanation of symbols, see Fig. 4.



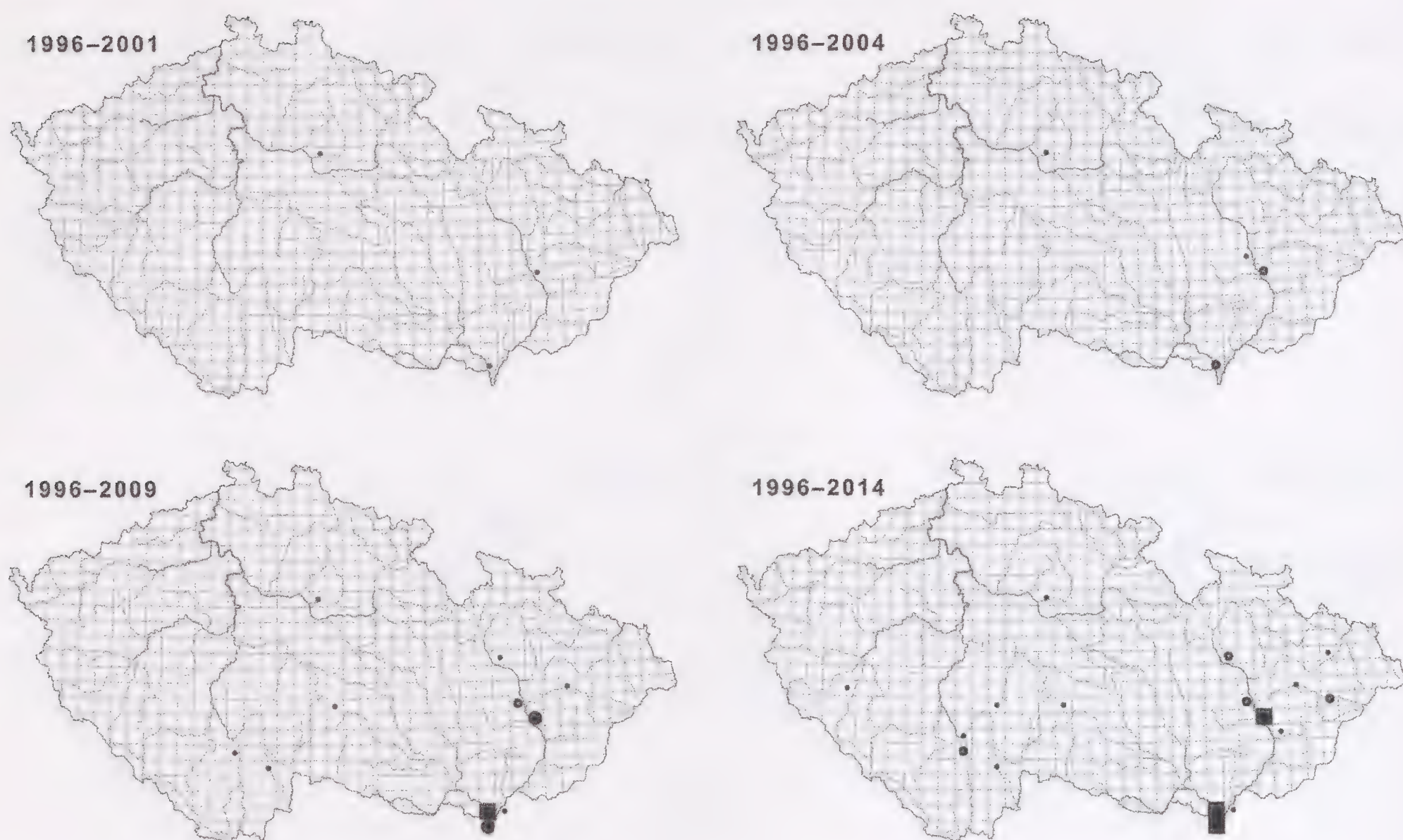


FIG. 10. Distribution of *Sinanodonta woodiana* records in mapping cells of the Czech Republic plotted in four time intervals. For explanation of symbols, see Fig. 4.

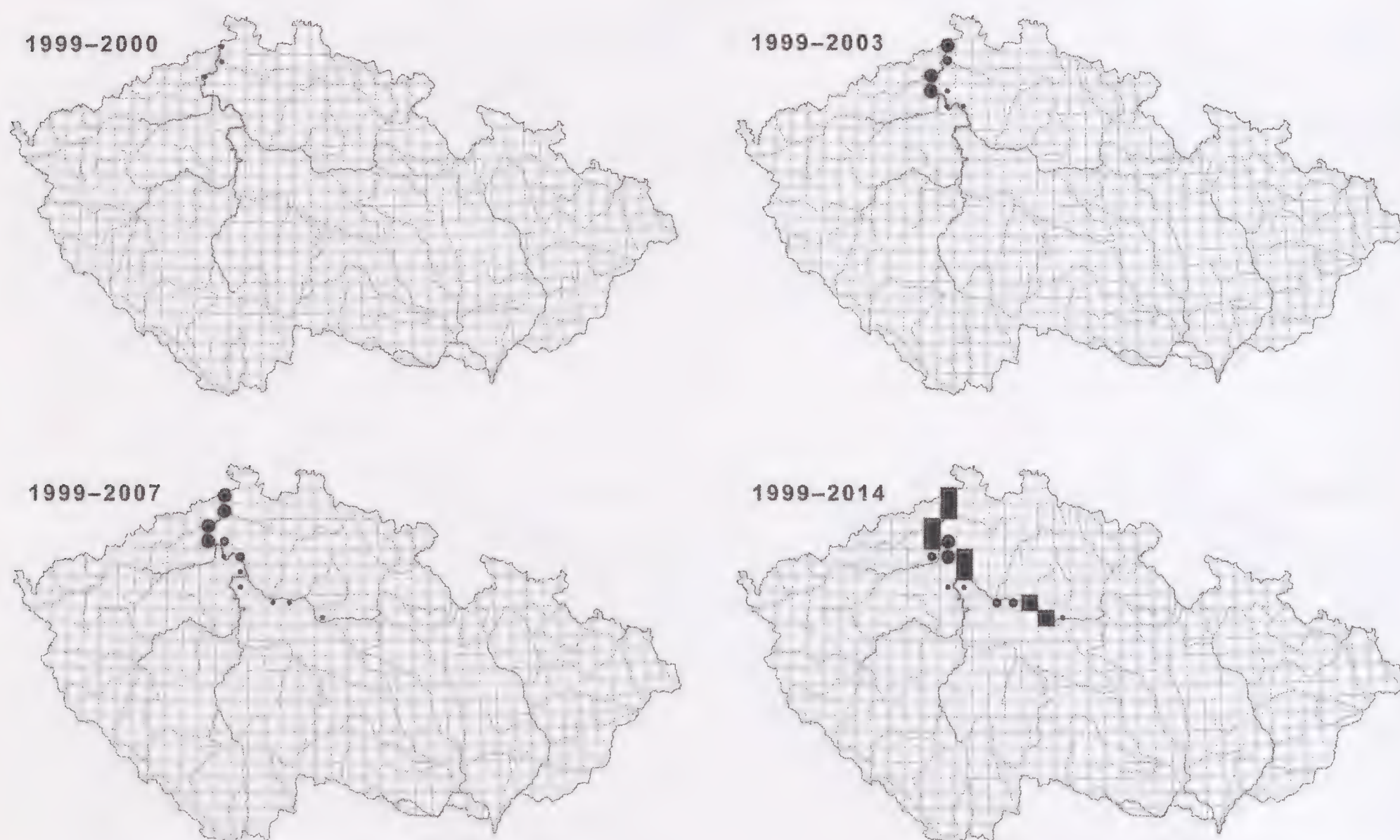


FIG. 11. Distribution of *Corbicula fluminea* records in mapping cells of the Czech Republic plotted in four time intervals. For explanation of symbols, see Fig. 4.



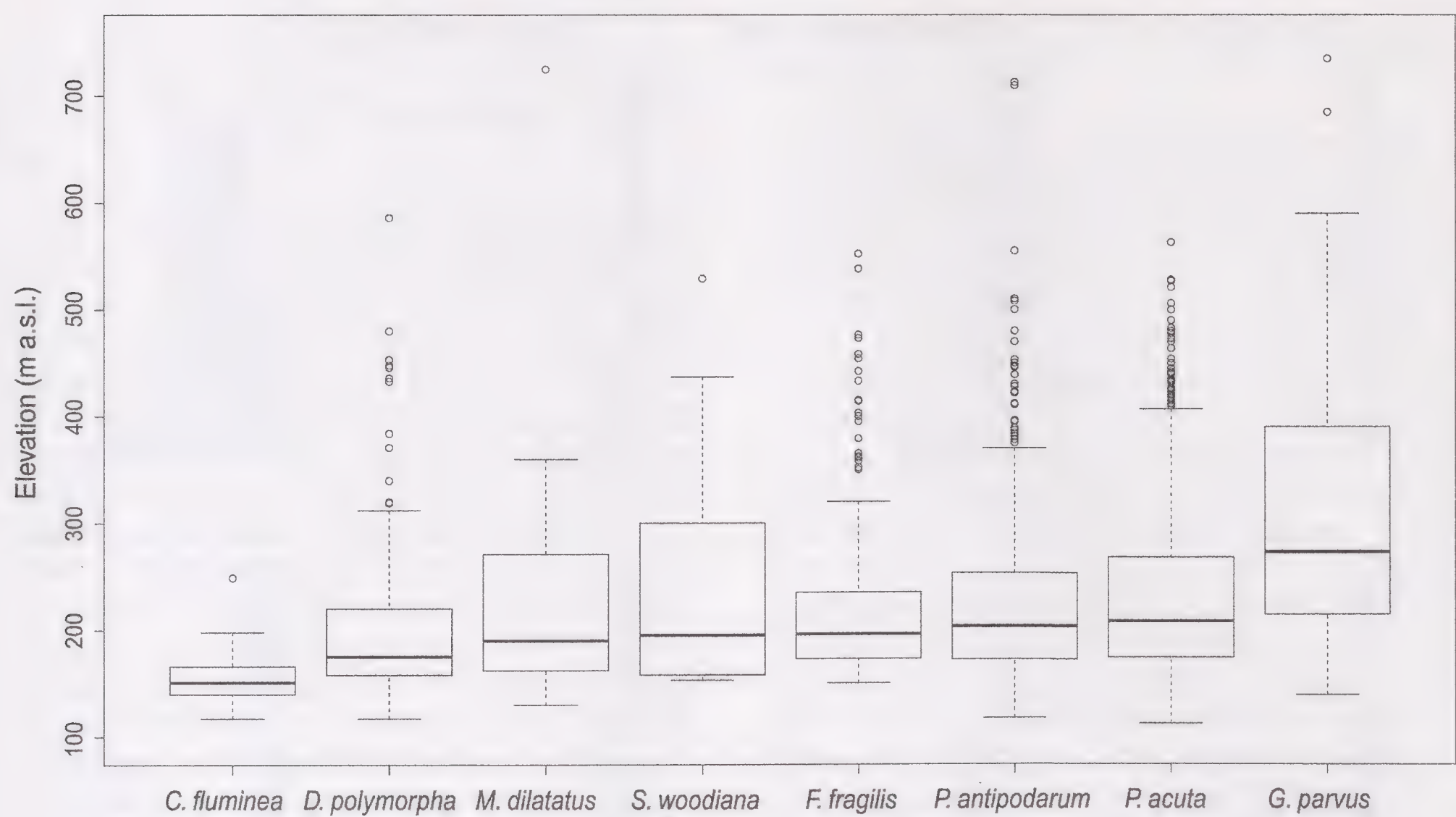


FIG. 12. Variation in elevation of sites with the records of eight non-native aquatic mollusc species occur in the Czech Republic: *Corbicula fluminea* (N = 105 sites), *Dreissena polymorpha* (N = 297), *Ferrissia fragilis* (N = 221), *Gyraulus parvus* (N = 123), *Menetus dilatatus* (N = 91), *Physella acuta* (N = 1001), *Potamopyrgus antipodarum* (N = 557), *Sinanodonta woodiana* (N = 48). For explanation of box-and-whisker plots see Fig. 2. Species are ordered based on median values.

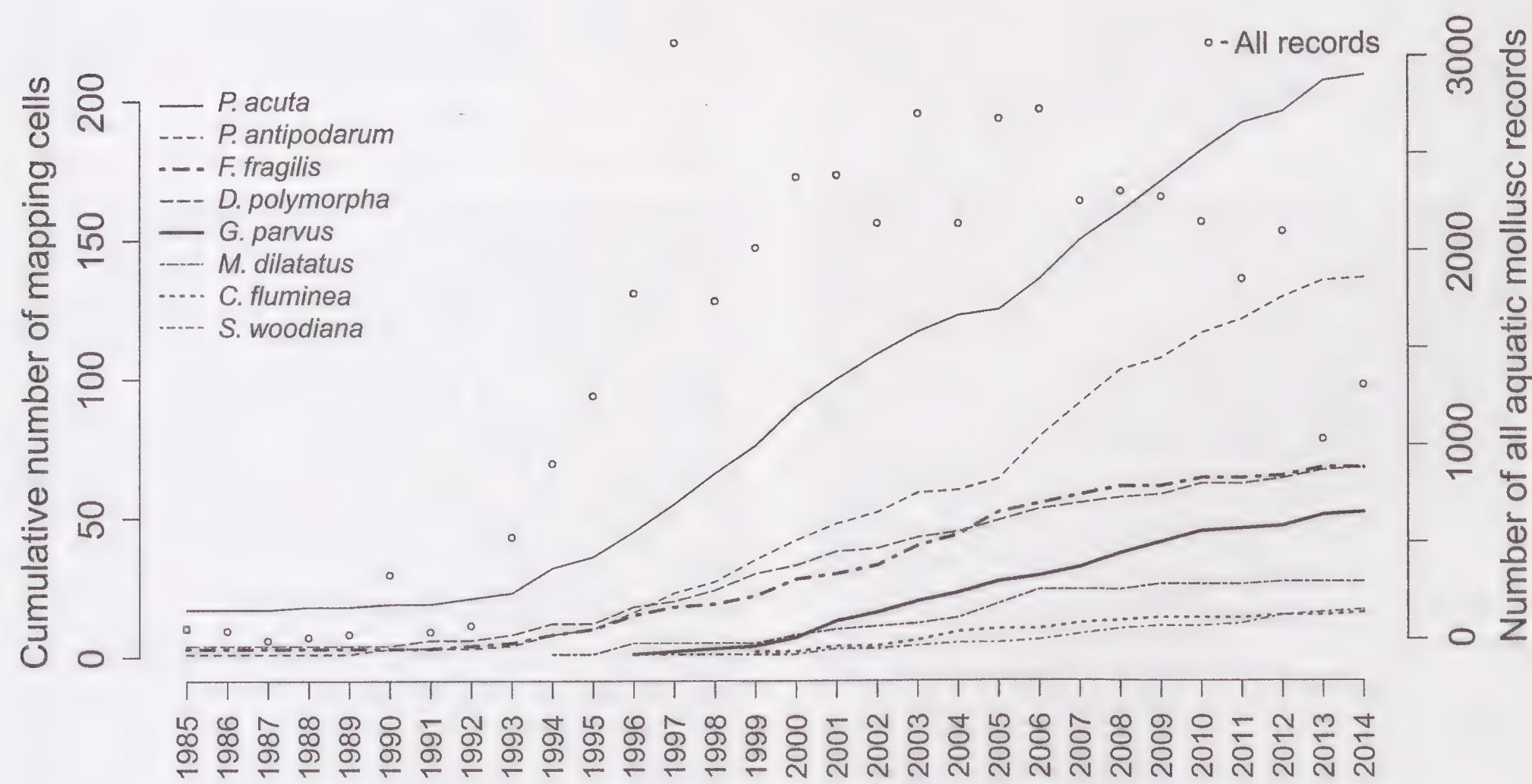


FIG. 13. Cumulative number of mapping cells with records of eight non-native aquatic mollusc species between 1985 and 2014. Number of records of all aquatic molluscs across the Czech Republic conducted in each year is shown by open dots with the scale given on the right side.



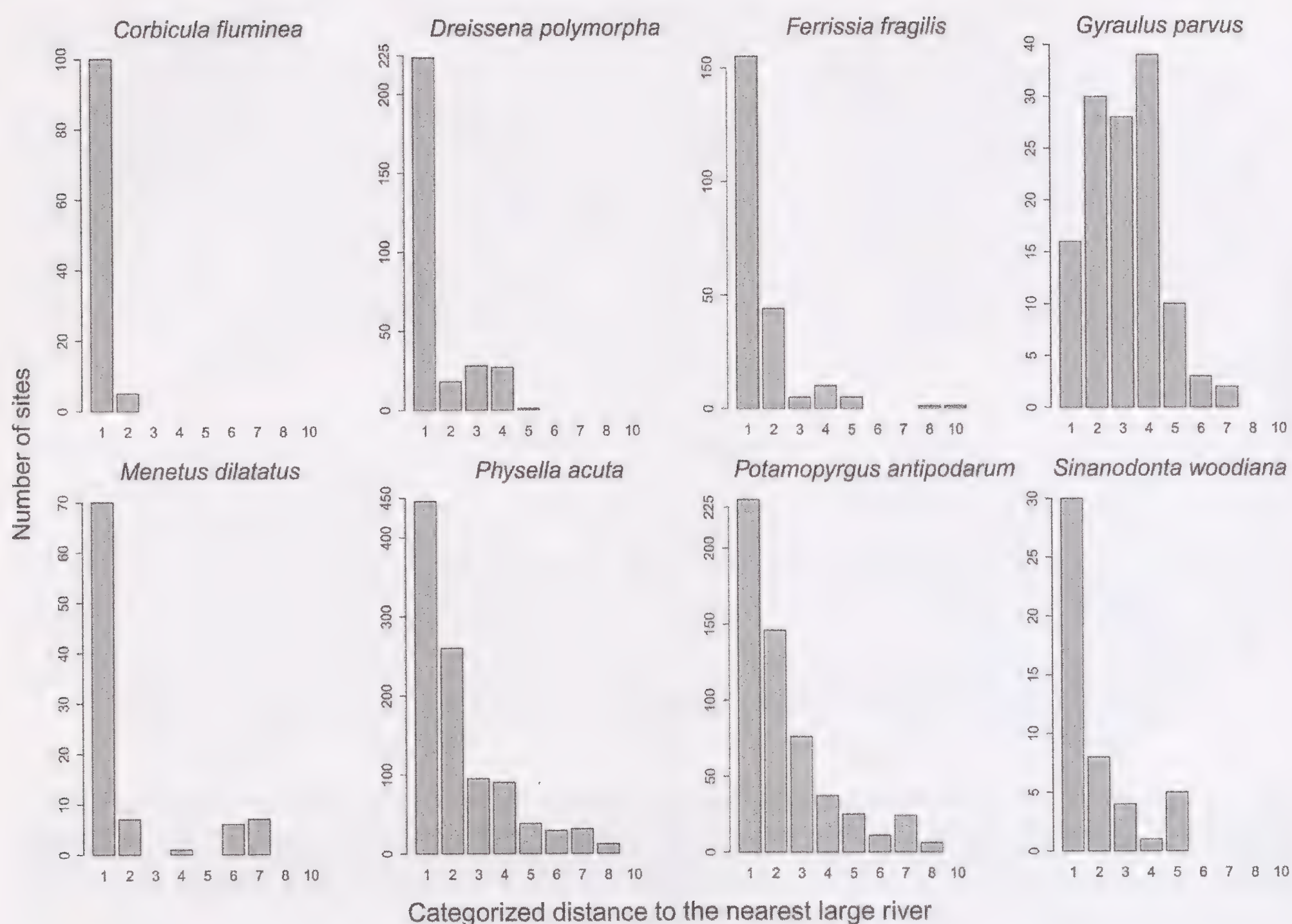


FIG. 14. Frequency of sites with the occurrence of the studied non-native species among 10 distance classes; the sites were assigned to the mapping grid cells which were categorized based on the distance to the nearest large river (1, the nearest; 10, the farthest; for details see Methods). Note that the scaling of y-axes differs among species.

of records sharply decreased towards higher elevation for all species, except for *Gyraulus parvus* (Fig. 12), as three-quarters of all species records were found between 112 and 254 m a.s.l. with the median value of 198 m a.s.l.

The oldest records out of all non-native water molluscs date back to 1891 for *Dreissena polymorpha* (by Blažka, 1893), to 1919 for *Physella acuta* (see Beran, 2002) (Figs. 4, 5) and to 1942 for *Ferrissia fragilis* (by Ložek, 1971) (Fig. 6). All the other species have been recorded since 1981 (Figs. 7–11). The fastest spreading was observed for *P. acuta* and *Potamopyrgus antipodarum* (Fig. 13), which were found in 27 and 20 new mapping cells, respectively, between 2009 and 2014. In contrast, two recent invaders (*Menetus dilatatus* and *Corbicula fluminea*) with much lower rate of colonisation were found in 1–2 new mapping cells over the same time period as the two former species. However, the other four species showing an intermediate rate

of colonization (i.e., 6–11 new mapping cells between 2009 and 2014) were for the first time recorded both 70 years ago (*D. polymorpha* and *F. fragilis*) and less than 20 years ago (*Gyraulus parvus* and *S. woodiana*).

We found that the number of non-native species recorded in mapping cells significantly decreased with the distance of the cells from the nearest large river ( $\rho = -0.40$ ;  $P < 0.001$ ). For all species the majority of their records belonged to the mapping cells that contain the 8<sup>th</sup>- and 9<sup>th</sup>-order river and the cells adjacent to these cells (very pronounced for *C. fluminea*, *F. fragilis* and *M. dilatatus*). *Gyraulus parvus* was the only exception showing a unimodal distribution of its records along the distance categories, with the highest number of its records assigned to the 4<sup>th</sup> grade cell category of the distance from the nearest larger river (see Materials and Methods). For details on individual species see Figure 14.



## DISCUSSION

## Number of Records in Time and Rate of Spreading

Using an extensive dataset of aquatic mollusc records from the Czech Republic, we observed a notable increase in the number of non-native species records since 1993. In 1990s, four newly introduced non-native species were recorded in the Czech Republic. For the most of the reported non-native species the expansion was found to be notably accelerating (Beran, 2002). Since 1993, however, there has also been a sharp increase in sampling effort (Fig. 13), which put the real rate of spreading into the question. We thus needed to interpret the increase in the occupancy of the target species with caution and to consider the data only once the sampling effort has been stabilised. This can be seen approximately since 1998 as the number of records of all aquatic mollusc species has reached 2000 per year (Fig. 13). Since that time, however, the number of newly invaded sites has still increased for several species (Fig. 13). The number of newly invaded mapping cells has remained stable since 1998, despite the decrease in sampling effort after 2006. Thus, we can conclude that older invaders are logically more widespread than the younger invaders, but also the rate of their spreading seems to be higher than that of the younger invaders. This is well supported especially for the two older invaders, *Physella acuta* and *Potamopyrgus antipodarum*. There is only one younger invader, *Gyraulus parvus*, which also experienced rather fast rate of spreading to new areas. In contrast, although being well monitored, the distribution of the rest of the younger invaders seems to be rather stable (*Menetus dilatatus*, since 2006) or relatively slowly increasing, once they had colonised most of areas with suitable habitats (*Corbicula fluminea*). The latter species, however, showed rather fast upstream spreading already at the beginning of its invasion (Beran, 2002, 2006b). It colonised a 83 km long stretch of the Elbe River between 1999 and 2003, and according to L. Beran's observation, the species moved upstream at least 2.4 km/year (Beran, 2006b). Based on the fact that the waterway transport is very limited in most of the Czech stretch of the Elbe River, the species is likely distributed on longer upstream-distances by waterbirds, as reported for some aquatic snails (Van Leeuwen et al., 2012, 2013).

## Current Distribution, First records and Habitat Affinities

*Physella acuta*, a species of North American origin, documented for the first time by J. Brabenec in 1919 (Beran, 2002), was found to be the most widely distributed species out of all non-native mollusc species reported from the Czech Republic (compare Fig. 5 with Figs. 4, 6–11). This is probably linked with its broad ecological niche as this species can inhabit various types of water bodies, being highly tolerant to eutrophicated, highly disturbed and artificial habitats (e.g., Serafinski, 1989; Wethington, 2004). The second most widely distributed species was *Potamopyrgus antipodarum*, a species of New Zealand origin, for the first time reported in 1981 (Kuchař, 1983), which was recorded mainly in the basins of the Elbe and Odra rivers. The highest frequency of its populations falls into the regions with a common occurrence of human-made biotopes (e.g., sandpits, other standing water bodies with gravelly and gravel-sandy bottom). In these areas of its widespread distribution, it can be also found in relatively undisturbed running waters (Beran, 2002; Horsák et al., 2013). A fairly fast spreading of this snail can be presumably attributed to its prevailing parthenogenetic reproduction in the areas out of its origin (Wallace, 1992).

Despite the fact that *Dreissena polymorpha* is the first recorded non-native species in the study area (found in 1891; Blažka, 1893), it expresses rather slow rate of spreading. This relatively low rate of invasion can be linked with the assumption that this species can be native in central Europe or at least it is not of a distinct origin (Stanczykowska, 1977). Known distribution can be at least partially biased by the fact that this mussel may occur up to the depth of 60 m (Zaiko & Olenin, 2006). A similar rate of spreading as for *D. polymorpha* was observed for *Ferrissia fragilis*. This species of North American origin, found for the first time in 1942 (Ložek, 1971), occurs mostly in standing waters, but recently it has also commonly invaded flowing-water habitats of large lowland rivers. It can be frequently also found in artificial warm waters as aquaria or pools in greenhouses (Beran, 2006a). *Gyraulus parvus* is also species of North American origin, reported for the first time in 1996 (Beran, 2000a). However, it is possible that at the beginning of its spreading it was confused with the native *G. laevis* (Beran, 2002). The



populations of *G. parvus* are scattered over the whole area mainly in human-made, highly altered water bodies. This species has been spreading rapidly since 2006 (Beran, 2006a) with an ability to colonise also higher altitudes, contrary to the other non-native species. Contrasting pattern of spreading than that of *G. parvus* was observed for *Menetus dilatatus*, also originating from North America, which was found for the first time in 1994 (Beran, 1994). At the beginning, it spread rather rapidly and saturated suitable habitats in a broader area of the Elbe River lowland, with the affinity to oxbow lakes and water bodies left after the mining. After 2003, a similar course of its invasion was observed in the upper Vltava River basin, where it inhabits an extensive system of dam water reservoirs (Beran, 2003, 2005). However, it has been found in only one new mapping cell since 2009.

*Sinanodonta woodiana*, a species of eastern Asia origin, was introduced with the stocking material of herbivorous fish species (e.g., silver carp, bighead carp and black carp) infected with glochidia (Horsák et al., 2010). Although it was found for the first time in 1996 (Beran, 1997), as was *G. parvus*, its spreading is notably slower (i.e., it was recorded from five times lower number of mapping cells in the first decade of the invasion) than that of *G. parvus*. This difference relates most likely to the mode of dispersal, which can be more effective for a small sized *G. parvus* with a potential for a passive dispersal mainly by waterbirds (Van Leeuwen et al., 2012). *Sinanodonta woodiana* has a scattered distribution in southern Moravia and southern Bohemia (Fig. 1), forming dense populations in some lowland rivers (Beran, 2013a) and dam water reservoirs (Horácková et al., 2014). Its glochidia can develop at various host fish, including many native species (Douda et al., 2012); thus, we can expect the acceleration of its spreading in future. A different scenario in comparison with the above species was found for the Asiatic *Corbicula fluminea*, for the first time recorded in 1999 (Beran, 2000b). After the first record in the Elbe River, it rapidly spread upstream, being able to colonise more than 200 km long stretch of the river over 15 years. Since that time, its spreading has dropped down notably, with rather slow rate of colonisation of downstream stretches of some tributaries (Beran, 2013b).

## Geographical Settings and Level of Invasion across the Czech Republic

Geographical position of the Czech Republic, situated in the basin of the three large European rivers (Elbe, Danube and Odra) and three main watersheds (North Sea, Baltic Sea and Black Sea), which were isolated till the 18<sup>th</sup> Century (Semenchenko et al., 2011), can play an important role in the spreading of non-native species. However, the fact that the study area includes mainly headwaters of these large rivers can slow down a potential pace of the spreading. Non-native species can spread both naturally (by a downstream drift or animal vectors) and by the human activities, especially shipping, but also aquaculture and fishing gear (e.g., Carlton, 1992; Pancucci-Papadopoulou et al., 2005). The construction of canals, artificially connecting previously separated biogeographic regions (Bij de Vaate et al., 2002), seems to be a primal threat for such hydrologically isolated regions as the Czech Republic.

The lowlands of the four largest rivers (Elbe, Odra, Morava and Dyje) and their surroundings were found to experience the highest level of the invasion (Figs. 1, 13, 14). Thus, we also found a significant and negative correlation between the number of non-native species recorded in mapping cells and the distance of the cells from the nearest large river for all studied species except *Gyraulus parvus*. In the Elbe River basin, six out of all eight non-native species were found in the Czech Republic for the first time (Beran, 2002). As the result, Bohemia (i.e., western part of the Czech Republic, mostly the Elbe River basin; Fig. 1) was invaded earlier by most of the species than Moravia (i.e., eastern part of the Czech Republic, Morava and Odra River basins). This indicates that the Elbe River is the most important corridor for the dispersal of non-native aquatic molluscs, which have been already introduced into the Western Europe, namely Germany. Similar conclusion was found by Nehring (2006), which showed that the Elbe River and the Danube River are responsible for introduction of 31 non-native macrozoobenthic species (including 11 molluscs) to Germany. Bódis et al. (2012) reported that 43 non-native species (including 11 molluscs) were introduced to Hungary throughout the Danube River.

In contrast, South Bohemia is generally the least invaded area out of all lowland regions,



with otherwise common non-native species still having only few records there (i.e., *P. acuta*, *P. antipodarum*, *F. fragilis* and *D. polymorpha*). As this region has been comparably explored as the other regions, the distributional pattern of non-native species is not only a product of insufficient sampling effort. The level of invasion also sharply decreased with elevation as most of the species populations occurred below 200 m a.s.l. Again, *G. parvus* was the only exception, as this species frequently inhabits also sites of middle elevations. Likewise, *S. woodiana* is more frequent in sites of middle elevations, which is probably linked with common occurrence of fish ponds in these areas.

We found that these eight non-native species in most cases invaded various types of standing habitats, except for natural standing water bodies less altered by humans, which were on the contrary the least invaded among the four main habitat types. The second most frequently invaded habitats were lowland rivers, which is the result of individual non-native species habitat affinities. The majority of them tended to prefer artificial and altered standing waters (especially *M. dilatatus* and *G. parvus*) and large rivers (especially *C. fluminea*). On the other hand, small rivers and brooks were frequently invaded only by *P. antipodarum* and less pronouncedly also by *P. acuta* (Fig. 3).

It is a common phenomenon that disturbed and human-made habitats, also characteristic of high propagule load, host more alien species than natural ones in terrestrial systems (Crawley, 1987; Vilà et al., 2007). Marine habitats highly altered by humans are also more invaded than the natural ecosystems (Bulleri & Airoldi, 2005; Glasby et al., 2007; Bulleri et al., 2010). Our data are in a concordance with these findings, as the highest frequency of non-native species records was observed in artificial standing water bodies. The artificial habitats are potentially more unstable and susceptible; thus, they are expected to be more prone to invasions than natural or semi-natural habitats (Crawley, 1987; Boggero et al., 2014). As these habitats are under a higher human pressure, it is more likely for a non-native species to be accidentally introduced there by human activities, for example, with the transferred fish and plant species, by transport associated with the modification of banks, and fishing gear to recreational water reservoirs (Cohen & Carlton, 1998; Albrecht et al., 2009; Van Leeuwen et al., 2013). However, Boggero et al. (2014) found that not the habitat type but temperature had

significant effect on the occurrence of non-native species. It is evident that key factors or habitat parameters that favour non-native species in inland water ecosystems are still poorly understood and we need more data for the prediction of their future distribution changes.

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INDIVIDUAL GROWTH IN THE PATAGONIAN GASTROPOD  
*BUCCINANOPS COCHLIDIUM* (NASSARIIDAE):  
A FIELD TAGGING-RECAPTURE EXPERIMENT

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ABSTRACT

This study describes the growth of individuals in a population of *Buccinanops cochlidium* (Nassariidae) through the identification of the best-fitting growth model based on field tag-recaptured experimental data. A total of 48 individuals (8.6% of total tagged snails) were recaptured after 2 to 25 months, representing a remarkable proportion for a field experiment with infaunal organisms. The sex ratio was not different from 1:1. Males measured between 63.4 and 89.0 mm ( $n = 25$ ), while females measured between 50.9 and 103.2 mm ( $n = 23$ ) in shell length. The maximum annual length increment obtained was 35.74 mm, mean annual length increment was 4.51 and 8.43 mm for females and males, respectively. Because no statistically significant differences were found between male and female growth increments, a single growth model was fitted to the entire data set.

Regarding individual growth modeling, the inverse Logistic (iLog) model adequately described the pattern in the data, but showed heteroscedasticity. A refitting of iLog using weighted least squares, weighted inverse Logistic (iLog\*), better fit the data (and agrees with biological knowledge of *B. cochlidium*) than the inverse Logistic (iLog), exponential (Exp), von Bertalanffy (vB) and Gompertz (Gz) models. Estimated parameters for the iLog\* model were  $\text{Max}\Delta L$ : 27.83,  $L_{50}$ : 69.89,  $L_{95}$ : 93.36. The results of this study are valuable for assessment of snail fisheries in Patagonia and suggest fisheries management policies for a sustainable future of this potential stock prior to extensive exploitation.

Key words: growth models, inverse logistic, edible snail, Nassariidae, fisheries, shells.

INTRODUCTION

Research about population parameters is a necessary first step in fisheries management (Botsford et al., 1998). Among them, growth models are a key component of stock assessments (Quinn & Deriso, 1999). Particularly for such difficult-to-age species as gastropods (Helidoniotis et al., 2011), crustaceans (Duran et al., 2013) and echinoderms (Russell & Meredith, 2000), size-based assessment models may be used to describe population dynamics instead of age-based models (Zhang et al., 2009).

Many organisms with calcareous parts, as mollusc shells, exhibit conspicuous growth band patterns. This may be due to annual cycles, although each case needs to be validated (Brey & Mackensen, 1997). However, in

many cases, observing and accurately counting these bands is very difficult; this is particularly true in some marine gastropods where bands are hidden by new shell growth or erased by sediment erosion. Tag-recapture experiments are a valuable approach to estimate growth parameters, but they are rarely used in invertebrates, including marine gastropods, despite the importance of growth characteristics as bioindicators, food resources, etc. (Appeldoorn, 1990; Henry & Jarne, 2007; Vasconcelos et al., 2006).

Among several individual growth functions, the von Bertalanffy (vB) growth model has been used historically as the default model in fisheries assessment (Beverton & Holt, 1959; Brey, 1999; Eveson et al., 2007; Frank, 1969). The vB model predicts a linear decline in growth rate as individuals get larger. Alternatively, the

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Gompertz (Gz) model predicts growth rates that initially rise for small individuals and then decline (Helidoniotis et al., 2011). However, these predictions are often not supported by data from juveniles. For some gastropod species, growth rate in juvenile stages was reported to remain constant rather than rising or dropping (Day & Fleming, 1992; Prince et al., 1988). The vB and Gz are deterministic growth functions that are probably not the best option for describing the growth of these size classes. The inverse Logistic (iLog) model was developed based on a modal analysis of length frequencies, and it suggests a constant growth rate for juvenile sizes. This model has been proposed as being biologically more appropriate for individual growth studies of some invertebrate species (Haddon et al., 2008; Helidoniotis et al., 2011; Ling et al., 2009; Starr et al., 2009). Previous studies on the individual growth of marine temperate gastropods tend to use vB model or exclude the iLog from the analysis (Arrighetti et al., 2012; Bigatti et al., 2007; Kideys, 1996; Vasconcelos et al., 2006; Zabala et al., 2013; among others).

The neogastropod *Buccinanops cochlidium* (Dillwyn, 1817) is endemic along the South American Atlantic coast between 23°00'S and 42°30'S. It reaches 110 mm in shell length and can weigh more than 100 g, which makes it the largest species of the genus and one of the largest members of the family Nassariidae (Abbott & Dance, 1986; Cernohorsky, 1984). Snail fisheries in Argentina have been focused mainly on volutid snails (Bigatti & Ciocco, 2008); *B. cochlidium* appears as a highly potential fisheries resource. The Argentinean *B. cochlidium* stock is abundant in sandy bottoms of shallow waters of North Patagonian gulfs, and is being commercially exploited at a small scale by artisanal fishermen for local consumption. However, extensive marine snail fisheries, including *Buccinanops* species, are starting to develop in response to international market requirements (Averbuj et al., 2010, 2014; Narvarte, 2006).

Most studies on *B. cochlidium* biology have mainly focused on its reproductive biology (Averbuj et al., 2010; Averbuj & Cremonte, 2010; Averbuj & Penchaszadeh, 2010; Penchaszadeh, 1971, 1973). Hatching size is only 4 mm in shell length (Averbuj & Penchaszadeh, 2010). Juveniles up to 25 mm are known to stay close to adults and take advantage of carrion generated by their predation to feed (Averbuj et al., 2012). Individuals reach reproductive

sizes at 60 mm (males) and 80 mm (females) in shell length (Averbuj et al., 2010). There are no studies on its growth. The sympatric species *B. globulosus* (Kiener, 1834) is presently commercially exploited (Narvarte, 2006); between 20 and 9,200 kg/year (2000–2004) of this species are captured in the San Matías Gulf (40°45'S, 64°00'W). It is locally consumed, as well as commercialized at small scale in Buenos Aires, Argentina, and is recently being exported to China (Averbuj et al., 2014).

The aim of this study was to describe the individual growth in a population of *Buccinanops cochlidium* through the identification of the best fitting growth model based on field tag-recapture experimental data. Goodness-of-fit tests and model selection techniques were used in order to provide some of the basic parameters of population dynamics. The results provide valuable information for assessment and future successful management of this valuable resource in North Patagonian Argentinean waters.

## MATERIAL AND METHODS

### Site Selection

The study was carried out at Playa Villarino, in Golfo San José (42°25'S, 64°31'W). All *Buccinanops cochlidium* individuals were captured by SCUBA diving at 5 to 10 m depth (low tides), approximately 1 km off the coastline.

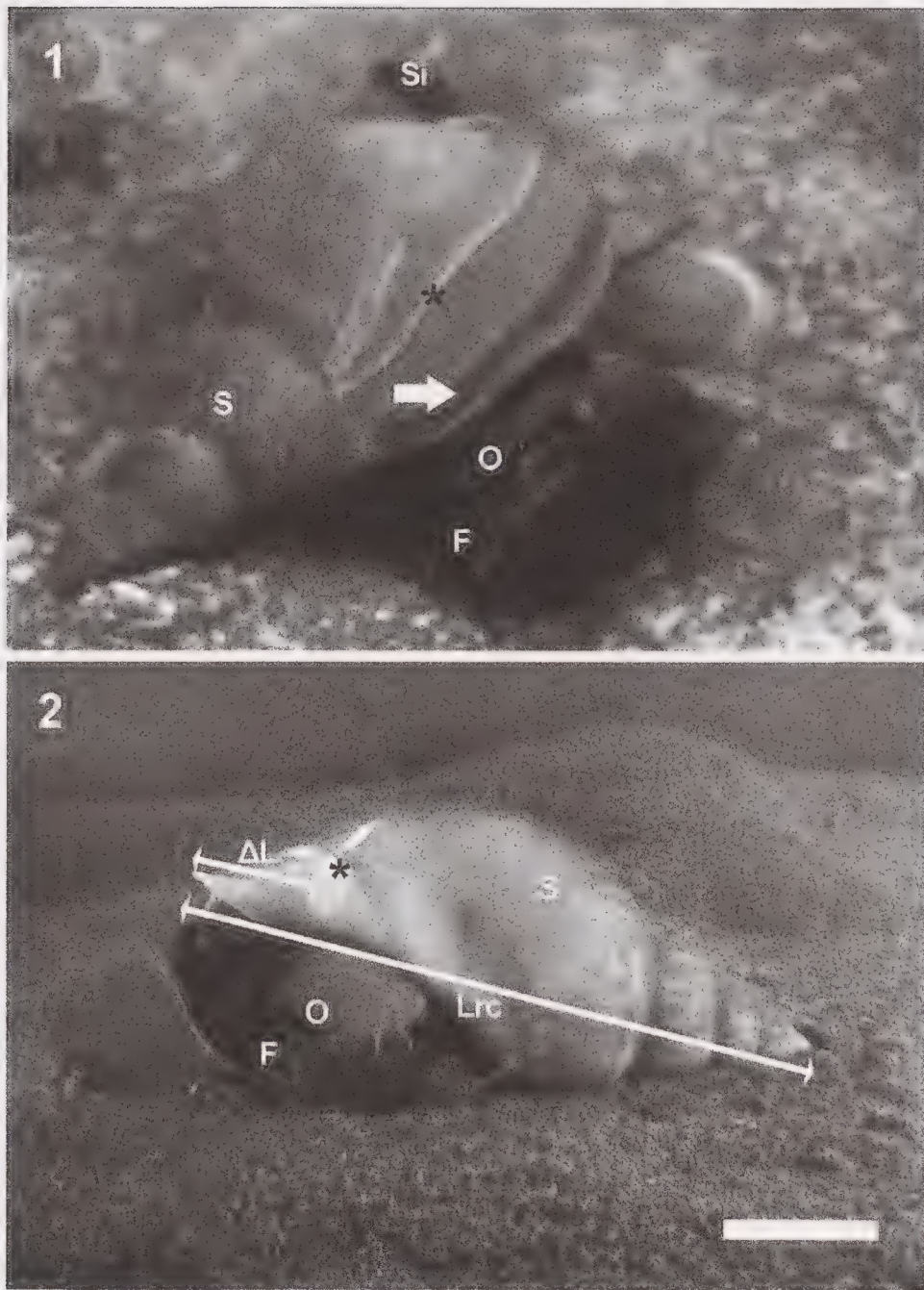
A total of 561 individuals of *B. cochlidium* were captured during 2006, in two sampling events: 261 snails in March and 300 snails in December. Each time, the Sampling Effort (SEf) was three divers (with a 12 l tank each, ~ 1 hour dives). All these snails were tagged and returned to field.

### Tag-Recapture Experiment

Prior to tagging, colonizing algae and/or encrusting organisms (mainly *Antholoba achates* anemones) were removed from the shells with a hard brush and the largest whorl of the shell was gently smoothed with fine sandpaper, rinsed in seawater and clean dried with absorbent paper.

Subsequently, the specimens were tagged by painting a line transverse to the growth direction, in the exterior of the outer lip of the shell's aperture, occupying the whole whorl wide at the latest CaCO<sub>3</sub> deposit of the shell (Fig. 1). Common nail paint was used to tag the shell





FIGS. 1, 2. *Buccinanops cochlidium*. FIG. 1: Individual with tagged shell; FIG. 2: Measurements made to the tagged individual at recaptured after 4 months. Abbreviations: Arrow - tag; F - foot; O - operculum; S - shell; Si - siphon;  $\Delta L$  - length increment;  $L_{rc}$  - length at recapture; \* - shell mark. Scale bar = 2 cm.

(Henry & Jarne, 2007), using red and white for differentiation of the two tagging events, in March and December 2006 respectively. After allowing the paint to dry completely, tagged individuals were rinsed in seawater to avoid desiccation or potential contamination due to paint residues, and returned to the field. Immediately after returning the tagged snails to the field and the following day, diving observations showed no tagged dead specimens in the area, indicating that the experiment treatment was not harmful to the snails. Previous aquarium assays (aerated seawater, conditioned at 35‰ salinity, and temperature ranging between 12°C and 14°C (spring temperature) on a 12:12 h light: dark photoperiod, similar to field measurements) showed that snails tagged with this technique survived for more than one year in conditioned aquaria, showing no eye visible adverse effect on the snails and good durability of the paint.

Recapture of tagged specimens was undertaken periodically after that, approximately at two-month intervals (depending on weather conditions), by hand gathering of three SCUBA divers, with a SEf equivalent to that of the original captures (at tagging). Recaptured specimens were measured in shell length (SL) (Fig. 2) with a digital calliper to the nearest 0.1 mm. The SL was considered at tagging,  $L_c$  (to the external edge of the nail paint tag) and recapture,  $L_{rc}$  (to the maximum size). Each individual was sexed by the presence or absence (female or male, respectively) of vagina and reproductive accessory glands. All recaptured individuals were kept for later studies, without returning them to the field, avoiding a second recapture of any individual.

### Growth Data

Because time at liberty was variable between individuals, we used individual length increments standardized by annual increment.

The sex ratio was analyzed with the Chi-square ( $\chi^2$ ) test. Difference in mean length at tagging ( $\overline{L_c}$ ), at recapture ( $\overline{L_{rc}}$ ) and mean length increments ( $\overline{\Delta L}$ ) between sexes was evaluated through Two Sample t-test using the *t.test* function implemented in R (R Development Core Team, 2009).

The data set used in this study can be found in Appendix A.

### Growth Models

Four non-nested candidate growth models were fitted to individual tag-recapture data (annual length increment;  $n = 48$  individuals) to identify the optimal model, in terms of statistical fit and parsimony, as descriptor of the individual growth process:

*von Bertalanffy (vB)*: This model implies that growth increments are a linear function of initial size.

*Gompertz (Gz)*: This model predicts a humped growth rate curve, with increasing growth rate for juveniles until a maximum and a decreasing growth rate for adult stage.

*Exponential (Exp)*: This model assumes a growth rate proportional to the initial length. An empiric function for individual growth increment data was used.

*inverse Logistic (iLog)*: This model implies constant growth increments in small individuals, and decreasing growth rate for intermediate sizes, until the growth increments are close to zero at larger sizes.



TABLE 1. Two samples t-test. Comparisons between sexes for mean length at capture and at recapture ( $\overline{L_c}$ ,  $\overline{L_{rc}}$ ), and mean growth increment ( $\overline{\Delta L}$ ), both in mm. Abbreviations: F - female; M - male; t - student statistic; df - degrees of freedom; CI - confidence intervals; S.D. - standard deviation;  $\alpha = 0.05$ .

| Parameter                    | F (S.D.)      | M (S.D.)     | t     | df | p-value | CI            |
|------------------------------|---------------|--------------|-------|----|---------|---------------|
| $\overline{L_c}$ (S.D.)      | 89.94 (10.93) | 76.13 (7.77) | 1.89  | 46 | 0.06    | [8.34; 19.30] |
| $\overline{L_{rc}}$ (S.D.)   | 91.97 (8.92)  | 80.16 (6.15) | 5.29  | 46 | < 0.001 | [7.29; 16.32] |
| $\overline{\Delta L}$ (S.D.) | 4.51 (2.63)   | 8.43 (3.35)  | -1.55 | 45 | 0.13    | [-9.02; 1.17] |

Models were fitted to length increment data (n = 48) using the Gauss-Newton algorithm, implemented in the function *nls* of the R program (R Development Core Team, 2009). As the iterative algorithm used in *nls* is sensitive to starting values, we selected an initial set of values for each growth function. The selection of these values was based on a preliminary data inspection of the parameters (considering its biological interpretation) obtained from the  $\Delta L$  vs  $L_c$  plot. This is a valid method when parameters of the proposed models have graphical interpretation (Pinheiro & Bates, 2000). The following values were identified, approximately: 22 mm for  $\Delta L_{Max}$ ; 70 mm for  $L_{50}$ ; 90 mm for  $L_{95}$ .

Selection among tested growth functions was based on two complementary criteria: (i) log-Likelihood or *LL* (best estimate); (ii) Akaike Information Criterion corrected for small sample size or *AICc* (adequate fit and parsimony (i.e., simple models are preferred to complex)).

To deal with heteroscedasticity, the selected growth function was refitted using weighted least squares. The improvement was evaluated by values of residual standard errors, where lower values represent better model performance.

For further explanations for mathematical models, see Appendix B.

RESULTS

Tag-Recapture Experiment

A total of 48 individuals (8.6% of total tagged snails) were recaptured after 2 (first recapture event) to 25 months (last recapture event), throughout 11 events (including the second marking event). The sex ratio of the sampled population of *Buccinanops cochlidium* was not



FIGS. 3–5. Growth measures comparison among sexes. FIG. 3: Length-at-capture; FIG. 4: Length-at-recapture; FIG. 5: Mean growth increments. Boxplots showing median, first and fourth quartiles and extreme lower and upper whisker; dots indicate outliers. Abbreviations:  $L_c$  - length-at-capture;  $L_{rc}$  - length-at-recapture;  $\Delta L$  - annual growth increments (all in mm).



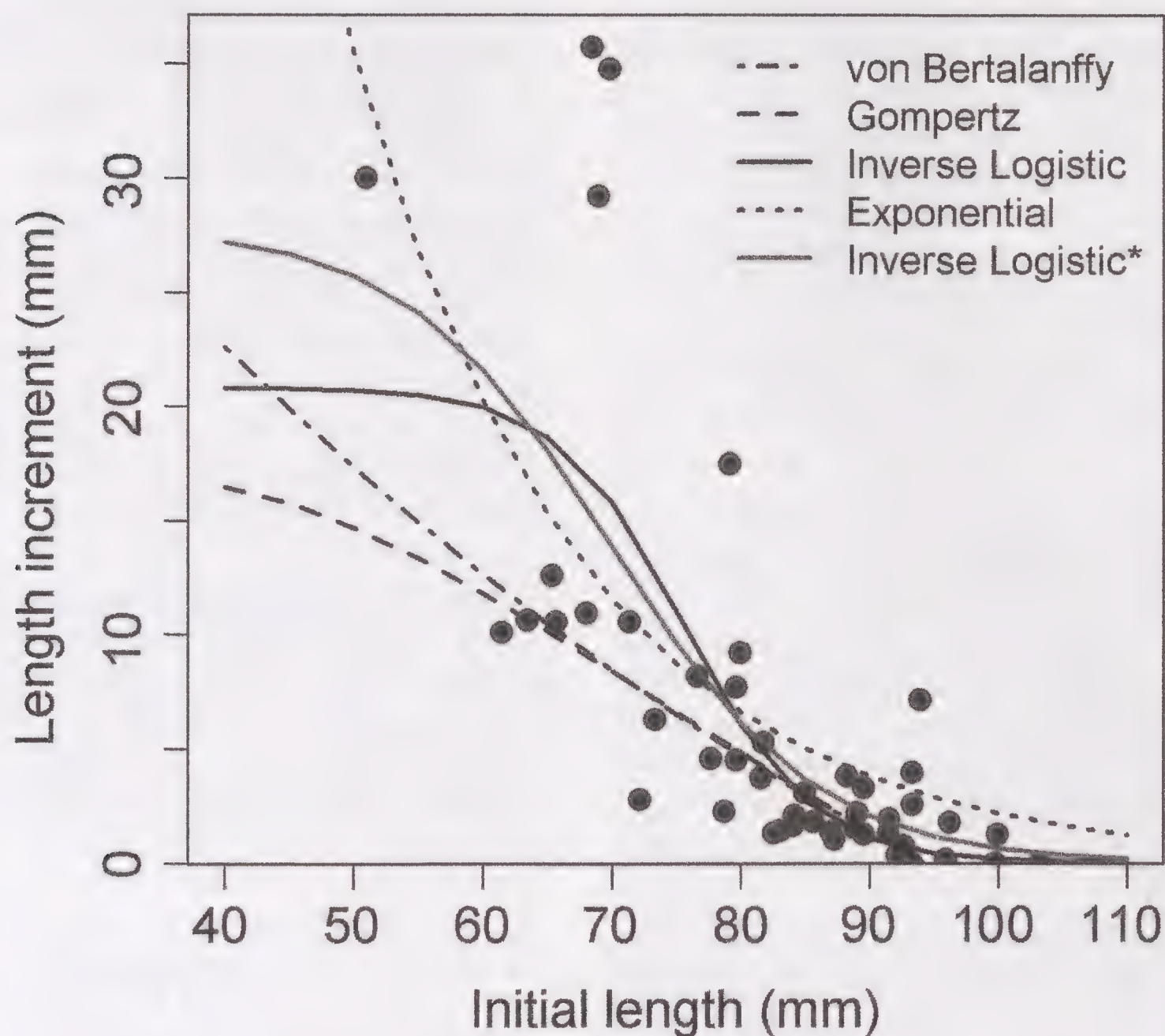


FIG. 6. The von Bertalanffy (vB), Gompertz (Gz), Exponential (Exp), inverse Logistic (iLog) and the weighted inverse Logistic (iLog\*) growth models fitted to growth increment data as function of initial length. Tag-recapture growth data ( $n = 48$  individuals); males (black spots) and females (grey spots) are plotted separately.

different from 1:1 ( $\chi^2 = 0.5$ ,  $df = 47$ ,  $p > 0.05$ ,  $n = 48$ ).

The 25 recaptured males measured between 63.4 and 89.0 mm, while the 23 females measured between 50.9 and 103.2 mm in shell length. Total shell size was significantly different

between males and females, both at tagging and at recapture (Table 1; Figs. 3, 4). The mean annual length increment was 4.51 mm and 8.43 mm for females and males, respectively. Because no significant differences were found between male and females for growth increments (Table 1; Fig. 5), a single growth model was fitted to the entire data set. The maximum annual length increment obtained was 35.74 mm.

#### Growth Models

Length increment data showed maximum and more variable values at smaller sizes (50–68 mm), followed by a decrease in the growth rate for intermediate sizes (70–92 mm) and a minimum for larger sizes (Fig. 6).

Among the four evaluated models, the iLog showed the best fit to data based on  $AIC_c$  and  $LL$  criteria (Table 2). This model captured well the pattern of the data: a constant growth rate in juvenile size classes followed by a non-linear

TABLE 2. Information criteria associated with statistical model selection. Five growth functions: von Bertalanffy, Gompertz, Exponential, inverse Logistic and weighted Inverse Logistic. Abbreviations:  $AIC_c$ , Akaike's Information Criterion corrected by small samples.

| Model                   | $LL$    | $AIC_c$ |
|-------------------------|---------|---------|
| <i>von Bertalanffy</i>  | -168.00 | 342.28  |
| <i>Gompertz</i>         | -168.18 | 342.63  |
| <i>Exponential</i>      | -156.59 | 319.45  |
| <i>inverse Logistic</i> | -153.80 | 316.15  |



TABLE 3. Residual error criterion for Inverse Logistic and weighted Inverse Logistic models.

| Model                            | Residual error (df) |
|----------------------------------|---------------------|
| <i>inverse Logistic</i>          | 6.16 (45)           |
| <i>weighted inverse Logistic</i> | 2.26 (45)           |

declining growth towards largest sizes (Fig. 6). The other growth models fitted the data and their biological interpretation worse. The Exp growth model fitted values slightly worse than those on iLog (Table 2); in addition, it predicted a maximum increment value of 583.28 mm. Gompertz and von Bertalanffy growth models failed to show a declining straight line, thus predicting negative increments for largest sizes (Fig. 6).

A residual graphical inspection over the selected iLog growth model showed heteroscedasticity in error terms (Fig. 7). The refit of the iLog growth function using weighted data (iLog\*) solved the heteroscedasticity problem and improved the fit (Table 3, Fig 8). Finally, from the selected version of the weighted iLog\* growth model, the estimated parameters predicted a

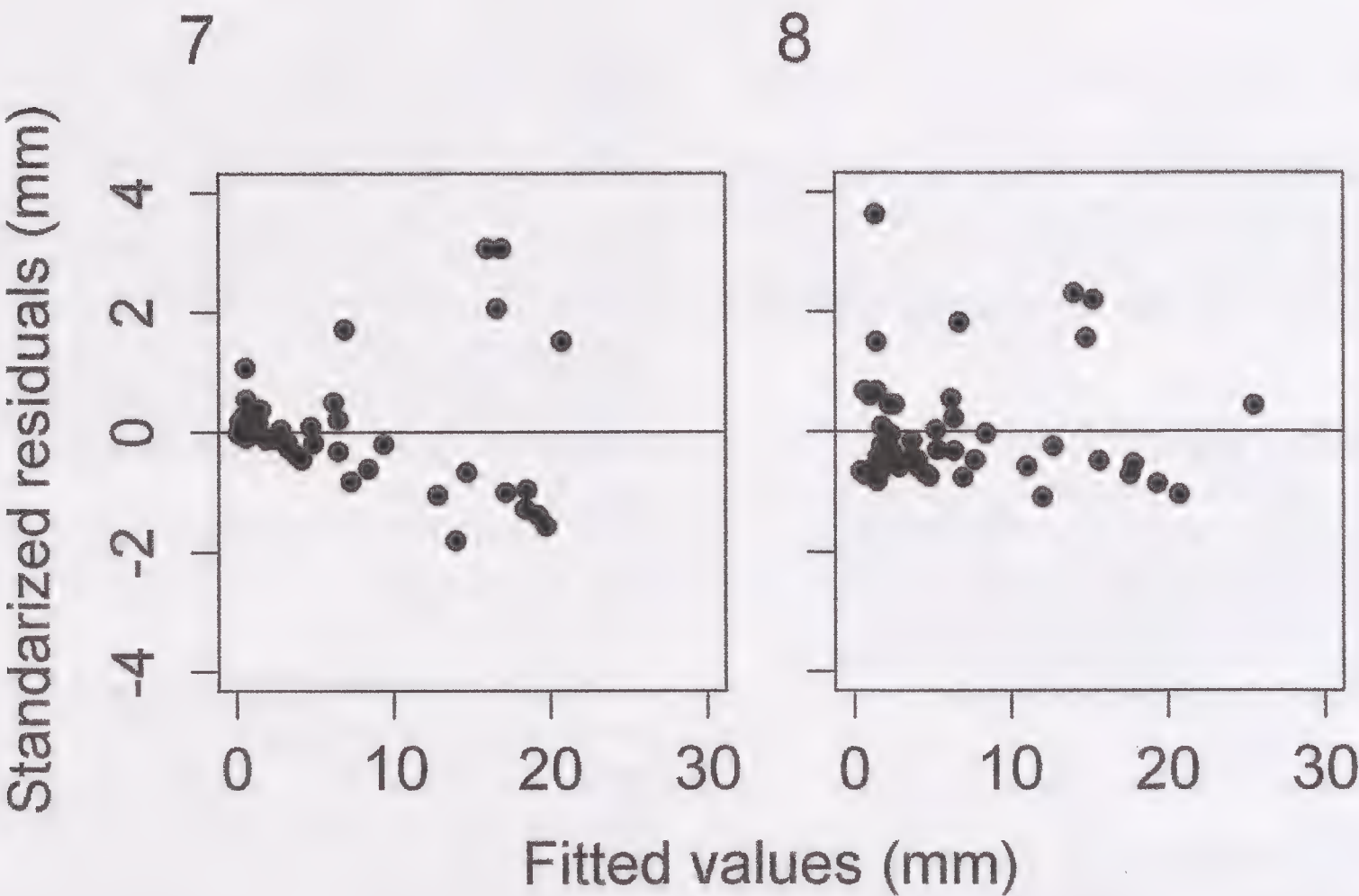
TABLE 4. Growth parameters for 48 length increment data (in mm) for the selected weighted Inverse Logistic growth model (iLog\*). Abbreviations: S.E., standard error.

| Parameter              | Estimate (S.E.) |
|------------------------|-----------------|
| <i>Max</i> $\Delta L$  | 27.83 (11.5)    |
| <i>L</i> <sub>50</sub> | 69.89 (7.29)    |
| <i>L</i> <sub>95</sub> | 93.36 (3.64)    |

maximum annual length increment( $\Delta L_{Max}$ ) of 27.83 mm; the initial length at which decline in growth rate is most rapid (*L*<sub>50</sub>) was 69.89 mm; and the lengths where growth increments become small (*L*<sub>95</sub>) was 93.36 mm. These parameters and their Standard Errors are included in Table 4.

DISCUSSION

Of 561 tagged individuals of *Buccinanops cochlidium* in this study, 48 were recaptured. This is a high recapture rate (~ 10%) for a subtidal marine open water study of infaunal mobile snails. Experiments in ponds or rocky



FIGS. 7, 8. Residuals analysis of the inverse Logistic model. FIG. 7: Variance assumed homogeneous; FIG. 8: Variance parameterized as inverse of squared predicted values from the original selected growth function.



shores have generated higher recapture rates (20–30%), including multiple recaptures (Vasconcelos et al., 2006; Eversole et al., 2008).

The pattern observed in the data shows that different processes occur through individual lifetimes in the analysed period. A non-linear growth pattern was evident: maximum growth increments occur at smaller sizes, then decrease at intermediate sizes, and minimum growth increments are observed at larger sizes. The weighted inverse Logistic (iLog\*) model most adequately described the growth pattern.  $L_{95}$  (initial length at 0.05 times  $\Delta L_{Max}$ ) estimation of the iLog\* is consistently close to the larger adult shell lengths in the studied population (Averbuj et al., 2010) where growth increments become small.  $L_{50}$  (initial length at 0.5 times  $\Delta L_{Max}$ ) of the iLog\* model represented the initial shell length at which the decline in growth rate turned most rapid (Haddon et al., 2008). Declines in growth rate are associated with the onset of maturity as energy is transferred from somatic growth to reproductive effort and a reduction in growth rate is expected (Lester et al., 2004). A strong correlation was found in abalone between size at maturity and  $L_{50}$  by Helidoniotis et al. (2011). This change occurred in *B. cochlidium* at ~ 60 mm (for males) and ~ 80 mm (for females) in shell length (Averbuj et al., 2010; Averbuj & Penchaszadeh, 2010). The  $L_{50}$  size from the iLog\* is 69.89 mm, which corresponds to an intermediate value between both supporting the use of the iLog\* model. These consistencies between the known and observed values with iLog\* model estimates support the use of the selected model as an adequate descriptor of the individual growth for *B. cochlidium* of Playa Villarino.

The Exponential (Exp) growth model is too simplistic to describe those processes. It assumes a constant decline growth rate that was not observed in the data. Furthermore, the residual analysis showed higher heteroscedasticity values in error terms, which were more difficult to statistically deal with, compared to iLog, as stated above (Escati-Peñaloza et al., 2010; Eveson et al., 2007). In the cases of von Bertalanffy (vB) and Gompertz (Gz),  $L_{\infty}$  represents the initial shell length where the predicted mean increment is zero, thus these models failed in the representation of the asymptotic maximum shell length which exhibited minimum growth increments (Ratkowsky, 1986). Instead,  $L_{\infty}$  represents the mean of the

distribution of maximum lengths for the population as a whole (Sainsbury, 1980). The vB and Gz growth models erroneously predicted negative growth increments at larger sizes. For further explanations of mathematical models see Appendix B.

Several studies have explored individual growth of marine snails, including a pioneering paper by Frank (1969) that focused on several tropical gastropods species. He tested the von Bertalanffy (vB) model, which explained correctly most of them. Most works since then have explained snails individual growth on the basis of vB function (Arrighetti et al., 2012; Frank, 1969; Ilano et al., 2004; Kideys, 1996; among others). Recently, alternative models explained better growth data of different gastropod species (Bigatti et al., 2007; Helidoniotis et al., 2011; Zabala et al., 2013). Among studies of marine gastropods growth based on tag-recapture data are scarce and commonly fitted vB model (Eversole et al., 2008; Vasconcelos et al., 2006). Nevertheless, studies of individual growth are essential for assessment and management of commercially exploited populations. Estimates of growth parameter are necessary as input parameters in many production models and stock assessments (Parma & Deriso, 1990; Quinn & Deriso, 1999).

The use of vB growth model is widely accepted in fisheries applications (Beverton & Holt, 1959; Brey, 1999; Eveson et al., 2007), frequently implemented by default without any previous analysis; thus, its adequacy has been questioned (Helidoniotis et al., 2011; Rogers-Bennett, 2003). Using the iLog (or iLog\*) growth model avoid negative increments predictions without requiring complicated probability density functions (*pdf*) (Eveson et al., 2007; Helidoniotis et al., 2011).

Obtaining a statistically optimum model can be possible by several arbitrary ways, for example by a polynomial function (Picado, 2009). Since often in ecology or fisheries management there is interest in understanding the mechanisms of the processes, the biological interpretation of the selected model becomes important. Exponential and inverse Logistic models had close values of selection criteria (iLog and iLog\* are both best fitted according to  $A/C_c$  and  $LL$ ). However, the iLog\* model shows a set of parameters that are biologically easier to understand, as explained above, that adds support to their use. Moreover, iLog (or its modified weighted inverse Logistic) model



showed the best fit, even through  $A/C_c$  criterion that penalizes the parameter number attending model parsimony.

Our study spanned the total range of individual sizes, although tagged juveniles (including small individuals under reproductive maturity up to 50 mm) were proportionally underrepresented in the growth analysis. Growth information from juvenile marine snails is difficult to obtain because small individuals are cryptic (Penchaszadeh et al., 2009), and also recapturing tagged juveniles becomes problematic owing to their mobility and high mortality rates (Gosselin & Pei-Yuan, 1997; Rogers-Bennett, 2003; among others). Despite this, the iLog\* growth model better represented the individual growth behavior than the other growth models evaluated, as it incorporated constant growth rate in juvenile size classes. Lacking data of those juvenile size classes may influence parameter estimations and, thus, time to enter the fishery; in particular, bias toward faster growth rates could lead to less precautionary management than should be considered (Rogers-Bennett, 2003).

Our data also show high variability at initial sizes, which could reveal an important feature of the studied population. Smaller individuals exhibit high variability in individual growth that could probably be related to the high plasticity of the organisms at these early stages. Saunders et al. (2009) demonstrate plasticity in growth traits of abalone, mainly related to food availability. Early life represents the most fragile stage in marine invertebrate life-history, in gastropods particularly, mortality rates are usually > 90% (Gosselin & Pei-Yuan, 1997). Survivorship depends on juveniles reaching critical sizes at which vulnerability to physical and biological constraints is substantially reduced (Gosselin & Pei-Yuan, 1997). Among survivors, food availability and other constraints would affect growth performance that may be expressed as a high variability at initial sizes. Juveniles of *B. cochlidium* feed on remains of prey captured by adults, thus facilitating food availability and survivorship (Averbuj et al., 2012).

The results of this study represent a valuable and original output as a first approach for assessment of nassariid snail fisheries in Patagonia. Also, the use of an alternative growth model may be a precedent for future studies in other regions that may benefit of our results.

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APPENDIX A. Data set used in this Study.

| ID | L1    | L2    | T1  | T2  | inc  | dT  | Sex | Lm     | dL         | dT.a       |
|----|-------|-------|-----|-----|------|-----|-----|--------|------------|------------|
| 1  | 65.6  | 69.6  | 1   | 139 | 4.0  | 138 | M   | 67.60  | 0.02898551 | 0.37808219 |
| 2  | 76.6  | 79.7  | 1   | 139 | 3.1  | 138 | M   | 78.15  | 0.02246377 | 0.37808219 |
| 3  | 79.6  | 81.3  | 1   | 139 | 1.7  | 138 | M   | 80.45  | 0.01231884 | 0.37808219 |
| 4  | 81.7  | 83.7  | 1   | 139 | 2.0  | 138 | M   | 82.70  | 0.01449275 | 0.37808219 |
| 5  | 84.9  | 87.2  | 1   | 274 | 2.3  | 273 | M   | 86.05  | 0.00842491 | 0.74794521 |
| 6  | 72.1  | 74.2  | 1   | 274 | 2.1  | 273 | M   | 73.15  | 0.00769231 | 0.74794521 |
| 7  | 68.0  | 76.2  | 1   | 274 | 8.2  | 273 | M   | 72.10  | 0.03003663 | 0.74794521 |
| 8  | 78.7  | 80.7  | 1   | 324 | 2.0  | 323 | M   | 79.70  | 0.00619195 | 0.88493151 |
| 9  | 83.0  | 84.5  | 1   | 383 | 1.5  | 382 | M   | 83.75  | 0.0039267  | 1.04657534 |
| 10 | 84.1  | 86.3  | 1   | 383 | 2.2  | 382 | M   | 85.20  | 0.00575916 | 1.04657534 |
| 11 | 77.6  | 82.4  | 1   | 383 | 4.8  | 382 | M   | 80.00  | 0.01256545 | 1.04657534 |
| 12 | 61.4  | 72.0  | 1   | 383 | 10.6 | 382 | M   | 66.70  | 0.02774869 | 1.04657534 |
| 13 | 87.2  | 88.3  | 1   | 383 | 1.1  | 382 | M   | 87.75  | 0.00287958 | 1.04657534 |
| 14 | 84.0  | 85.7  | 1   | 383 | 1.7  | 382 | M   | 84.85  | 0.00445026 | 1.04657534 |
| 15 | 73.3  | 79.9  | 1   | 383 | 6.6  | 382 | M   | 76.60  | 0.01727749 | 1.04657534 |
| 16 | 87.0  | 89.0  | 1   | 544 | 2.0  | 543 | M   | 88.00  | 0.00368324 | 1.48767123 |
| 17 | 82.5  | 85.3  | 1   | 771 | 2.8  | 770 | M   | 83.90  | 0.00363636 | 2.10958904 |
| 18 | 79.1  | 81.4  | 274 | 322 | 2.3  | 48  | M   | 80.25  | 0.04791667 | 0.13150685 |
| 19 | 68.4  | 73.1  | 274 | 322 | 4.7  | 48  | M   | 70.75  | 0.09791667 | 0.13150685 |
| 20 | 63.4  | 64.8  | 274 | 322 | 1.4  | 48  | M   | 64.10  | 0.02916667 | 0.13150685 |
| 21 | 71.3  | 74.4  | 274 | 381 | 3.1  | 107 | M   | 72.85  | 0.02897196 | 0.29315068 |
| 22 | 79.9  | 82.6  | 274 | 381 | 2.7  | 107 | M   | 81.25  | 0.02523364 | 0.29315068 |
| 23 | 68.9  | 82.2  | 274 | 440 | 13.3 | 166 | M   | 75.55  | 0.08012048 | 0.45479452 |
| 24 | 79.6  | 83.1  | 274 | 440 | 3.5  | 166 | M   | 81.35  | 0.02108434 | 0.45479452 |
| 25 | 65.3  | 76.5  | 274 | 598 | 11.2 | 324 | M   | 70.90  | 0.0345679  | 0.88767123 |
| 26 | 93.3  | 94.8  | 1   | 139 | 1.5  | 138 | H   | 94.05  | 0.01086957 | 0.37808219 |
| 27 | 93.9  | 96.6  | 1   | 139 | 2.7  | 138 | H   | 95.25  | 0.01956522 | 0.37808219 |
| 28 | 88.8  | 89.5  | 1   | 169 | 0.7  | 168 | H   | 89.15  | 0.00416667 | 0.46027397 |
| 29 | 85.6  | 87.2  | 1   | 324 | 1.6  | 323 | H   | 86.40  | 0.00495356 | 0.88493151 |
| 30 | 91.5  | 93.2  | 1   | 324 | 1.7  | 323 | H   | 92.35  | 0.00526316 | 0.88493151 |
| 31 | 88.2  | 92.2  | 1   | 383 | 4.0  | 382 | H   | 90.20  | 0.0104712  | 1.04657534 |
| 32 | 93.3  | 96.4  | 1   | 442 | 3.1  | 441 | H   | 94.85  | 0.00702948 | 1.20821918 |
| 33 | 89.5  | 91.8  | 1   | 666 | 2.3  | 665 | H   | 90.65  | 0.00345865 | 1.82191781 |
| 34 | 91.4  | 94.1  | 1   | 771 | 2.7  | 770 | H   | 92.75  | 0.00350649 | 2.10958904 |
| 35 | 92.6  | 92.7  | 274 | 322 | 0.1  | 48  | H   | 92.65  | 0.00208333 | 0.13150685 |
| 36 | 99.7  | 99.7  | 274 | 322 | 0    | 48  | H   | 99.70  | 0          | 0.13150685 |
| 37 | 103.2 | 103.2 | 274 | 322 | 0    | 48  | H   | 103.20 | 0          | 0.13150685 |
| 38 | 99.7  | 99.7  | 274 | 322 | 0    | 48  | H   | 99.70  | 0          | 0.13150685 |
| 39 | 93.2  | 93.2  | 274 | 322 | 0    | 48  | H   | 93.20  | 0          | 0.13150685 |
| 40 | 69.8  | 80.0  | 274 | 381 | 10.2 | 107 | H   | 74.90  | 0.0953271  | 0.29315068 |
| 41 | 50.9  | 59.7  | 274 | 381 | 8.8  | 107 | H   | 55.30  | 0.08224299 | 0.29315068 |
| 42 | 92.1  | 92.2  | 274 | 381 | 0.1  | 107 | H   | 92.15  | 0.00093458 | 0.29315068 |
| 43 | 81.5  | 82.6  | 274 | 381 | 1.1  | 107 | H   | 82.05  | 0.01028037 | 0.29315068 |
| 44 | 89.0  | 90.0  | 274 | 440 | 1.0  | 166 | H   | 89.50  | 0.0060241  | 0.45479452 |
| 45 | 89.5  | 91.0  | 274 | 440 | 1.5  | 166 | H   | 90.25  | 0.00903614 | 0.45479452 |
| 46 | 95.9  | 96.0  | 274 | 477 | 0.1  | 203 | H   | 95.95  | 0.00049261 | 0.55616438 |
| 47 | 99.9  | 101.0 | 274 | 598 | 1.1  | 324 | H   | 100.45 | 0.00339506 | 0.88767123 |
| 48 | 96.2  | 98.6  | 274 | 769 | 2.4  | 495 | H   | 97.40  | 0.00484848 | 1.35616438 |



## APPENDIX B. Detailed Explanations of Mathematical Models.

Individual length increments standardized year

$$(1) \Delta L = \frac{L_{rc} - L_c}{\Delta t_a}; \quad \Delta t_a = (t_{rc} - t_c)/365$$

were  $\Delta L$  is the standardized length increment,  $L_{rc}$  the length at recapture,  $L_c$  the length at tagging,  $\Delta t_a$  represent the time at liberty relative to an annual period with  $t_{rc}$  as time at recapture and  $t_c$  the time at tagging.

*von Bertalanffy (vB)*. This model implies that growth increments are a linear function of initial size. A re-parameterized version for tag-recaptured data was used (Fabens, 1965),

$$(2) \Delta \hat{L}_i = (L_\infty - L_{ci})(1 - e^{-k\Delta t_a}) + \varepsilon$$

*Gompertz (Gz)*. This model predict a humped growth rate curve, with increasing growth rate for juveniles until a maximum and a decreasing growth rate for adult stage

$$(3) \Delta \hat{L}_i = L_\infty \left( \frac{L_{ci}}{L_\infty} \right)^{e^{-\Delta t_a}} - L_i + \varepsilon$$

*Exponential (Exp)*. This model assumes a growth rate proportional to the initial length. An empiric function for individual growth increment data was used

$$(4) \Delta \hat{L}_i = \text{Max}\Delta L_{ci} e^{-cL_{ci}} + \varepsilon$$

*Inverse Logistic (iLog)*. This model implies constant growth increments in small individuals, and decreasing growth rate for intermediated sizes, until the growth increments are close to zero at larger sizes

$$(5) \Delta \hat{L}_i = \frac{\text{Max}\Delta L_i}{1 + e^{\frac{\ln(19) \frac{L_{ci} - L_{50}}{L_{95} - L_{50}}}}} + \varepsilon$$

where  $\Delta \hat{L}_i$  represent the expected length increment for individual  $i$ ,  $L_\infty$  the asymptotic length (vB and Gz),  $L_{ci}$  the length at tagging (initial length) for individual  $i$ ,  $k$  is the growth parameter (vB),  $g$  and  $c$  is the rate of change in length increment (Gz and Exp, respectively),  $\Delta t_a$  is the time at liberty as annual fraction (vB and Gz),  $\text{Max}\Delta L_i$  is the maximum length increment,  $L_{50}$  is the initial length at 0.5 times  $\text{Max}\Delta L_i$  and  $L_{95}$  is the initial length at 0.05 times  $\text{Max}\Delta L_i$ .

The term  $\varepsilon$  represents process stochasticity, and is an independent additive normal random error term.

## Selection complementary criteria

Selection among tested growth functions was based on two complementary criterions:

(i) log-Likelihood. The model which presents the greatest estimate for the log-Likelihood will best represent the data. For this criterion, as more parameters are incorporated into the model, uncertainty will be lower and higher the degree of explanation (Burnham & Anderson, 2002).

Through this function the negative log-Likelihood ( $LL$ ) was minimized for each fitted growth function,

$$(6) -LL = -\frac{1}{2}n \log \left[ \frac{\sum_{i=1}^n (\Delta L_i - \Delta \hat{L}_i)^2}{n} \right]$$

where  $\Delta L_i$  is the observed length increment for each of the  $i=1$  to  $n$  observations and  $\Delta \hat{L}_i$  is the expected length increment for observations  $i$  for one of the four candidate growth models;  $(\Delta L_i - \Delta \hat{L}_i)$  differences is the produced error among predicted and observed growth increment due to the fit of each growth function to data.

(ii) Akaike Information Criterion corrected for small sample size ( $AIC_c$ ). This version of  $AIC$  is recommended for cases in which the ratio between sample size and number of estimated parameters is less than 40 (Burnham & Anderson, 2002); This technique is frequently used for models selection in mark-recaptured studies (Johnson & Omland, 2004). According to  $AIC$ , the model with the smallest value will present the best fit to the data among the candidate models considered (Quinn & Deriso, 1999). Finally,  $AIC_c$ :

$$(7) AIC_c = -2\log(L) + 2k \left( \frac{n}{n-k-1} \right)$$

were  $L$  is the Likelihood,  $k$  is the number of parameters to estimate and  $n$  is the sample size. We used  $AIC$  because it allows selection among models based on adequate fit and



parsimony (e.i., simple models are preferred to complex).

To deal with heterocedasticity, the selected growth function was refitted using weighted least squares

$$(8) \quad w_i = \frac{1}{(\hat{y}_i)^2}$$

where  $w_i$  represented the weight given to each  $\hat{y}_i$  predicted values from the original selected

growth function. The improvement was evaluated by values of residual standard errors, where minor values represent better model performance.

To confirm starting values for iLog model fitting, several ( $n = 60$ ) fits were generated using different sets of starting values (combinations), and collected the final estimates (see Complementary data section), then the mean and sd for this distribution of generated estimates was compared with the original analysis.







TAXONOMIC REVISION OF THE ANATOMIDAE (MOLLUSCA:  
GASTROPODA: VETIGASTROPODA) FROM BRAZIL,  
WITH DESCRIPTION OF FOUR NEW SPECIES

Alexandre Dias Pimenta<sup>1\*</sup> & Daniel L. Geiger<sup>2</sup>

ABSTRACT

A taxonomic revision of the family Anatomidae from Brazil led to the discovery of nine species, four of which are new. This contrasts with only two species previously recorded: *Anatoma aedonia* (Watson, 1886) and *Anatoma proxima* (Dall, 1927). The lectotype designation for *A. aedonia* by Geiger (2012) has clarified the identity of this taxon, which is now considered a rare species, mainly from deep waters. The holotype of *A. proxima* is lost (Geiger, 2012), and some very similar taxa occur sympatrically in the western Atlantic; accordingly, we designate here a neotype for *Scissurella proxima* and redescribe it, re-evaluating its shell variability and radula morphology. The review of a large amount of shells in malacological collections in Brazil, including material from recent dredging along the southeastern coast, revealed the occurrence of seven additional species: *Anatoma americana* Bandel, 1998, synonymized under *A. proxima* by Geiger (2012), is herein considered a valid species; *Anatoma atlantica* (Bandel, 1998); and *Anatoma alternatisculpta* Geiger & McLean, 2010. Those three species were only known from the Caribbean region and are now recorded from Brazil. Four new species are described: ***Anatoma espiritosantense***, n. sp., diagnosed by a trochiform to globose shell with irregularly distributed axial ribs over the shoulder, is restricted to the southeastern coast of Brazil; ***Anatoma campense***, n. sp., characterized by a biconical shell, a well projecting keel of the selenizone, and a strong spiral cord on teleoconch I, is rare, restricted to the south-southeastern coast of Brazil; ***Anatoma brychia***, n. sp., the deepest species from Brazil (~ 1,900 m), is diagnosed by its longer teleoconch I, with 1.25 whorls and tiny sculpture; ***Anatoma copiosa***, n. sp., is abundant, with several records from the southeastern coast of Brazil; it is distinguished from *A. atlantica* by the very faint axial ribs on the base of the shell. An eleventh likely undescribed taxon, *Anatoma* sp., is recorded based on a single shell, distinguished by a globose shell, faint spiral sculpture, and long teleoconch I.

Key words: taxonomy, western Atlantic, marine molluscs, neotype, *Anatoma proxima*.

INTRODUCTION

Anatomidae comprises a group of minute (1–10.5 mm: mode 2–3 mm) marine gastropods of worldwide distribution, mostly from the continental shelf to the deep sea (Geiger & Sasaki, 2009). The family is composed of two genera: *Anatoma* Woodward, 1859 [= *Thielella* Bandel, 1998: see Høisaeter & Geiger, 2011) and the monotypic *Sasakiconcha* Geiger, 2006. Knowledge of the taxonomy and diversity of Anatomidae has increased considerably in the past fifteen years, with several works on its systematics (e.g., Bandel, 1998; Geiger,

2003, 2006a–c, 2008; Geiger & Fernández-Gracés, 2010; Geiger & Jansen, 2004a, b; Geiger & Marshall, 2012; Geiger & McLean, 2010; Geiger & Sasaki, 2008; Høisaeter & Geiger, 2011; Marshall, 2002; Sasaki et al., 2010; Zelaya & Geiger, 2007). These papers included the description of several new species, most of them from the Indo-Pacific region. A synthesis of the taxonomy and diversity of Anatomidae was recently published by Geiger (2012), who considered 79 species valid in the genus *Anatoma*.

The greatest diversity of *Anatoma* is found in the Indian and Pacific oceans, with 51 spe-

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cies. The North Atlantic is also a rich area, with 15 species, and the Caribbean region includes eight species, while in the western Atlantic as a whole (from Canada to South Argentina), there are ten species. These numbers contrast to the low counts of *Anatoma* species from Brazil, where *Anatoma aedonia* (Watson, 1886) and *Anatoma proxima* (Dall, 1927) were the only two species recorded (Geiger, 2012).

Collection-based studies, as well as on material from several recent sampling expeditions in Brazil, especially along the southeastern coast, aiming to catalogue the marine biodiversity, revealed that the name *Anatoma aedonia* has been applied to ten different taxa, which are the focus of this paper.

## MATERIAL AND METHODS

The taxonomic identifications were based on conchological comparisons with original descriptions and illustrations, as well as all extant type material, most of which has been illustrated in Geiger (2012).

Most of the material from Brazil here studied was collected off its central/southeastern coast during the following oceanographic expeditions: MD55 – a French-Brazilian Expedition conducted in May/June 1987 along the Vitória-Trindade chain of seamounts in southeastern Brazil (~ 21°S), from *Research Vessel Marion-Dufresne*; “REVIZEE Score Central – Programa de Avaliação do Potencial Sustentável de Recursos Vivos da Zona Econômica Exclusiva” (Program of Evaluation of the Sustainable Potential of Living Resources in the Economic Exclusive Zone), carried out by Ministério do Meio Ambiente, Brazilian Government, from 1996 to 2001, which collected at several stations between Salvador (Bahia state, ~ 13°S) and Cabo de São Tomé (Rio de Janeiro state, ~ 22°S), from modified supply boat *Astro Garoupa* and Oceanographic Ship *Antares*; Oceanprof – step of “Environmental Characterization of Campos Basin, RJ, Brazil”, carried out by Petrobras in 2002/2003; HAB – “Projeto Habitats, Heterogeneidade Ambiental da Bacia de Campos” (Habitats Project, Campos Basin Environmental Heterogeneity), by CENPES/ Petrobras in 2008/2009, both carried out at several localities and depths in the Campos Basin, Rio de Janeiro state (~ 21°S to 24°30’S), from oceanographic ship *Miss Emma McCall*.

Given the recent monograph by Geiger (2012), only additional material is listed here, except when a particular lot was re-examined to verify previous identifications. In the material examined lists, numbers in brackets indicate number of shells in each lot; most of the material consisted of empty shells; the few cases of wet-preserved specimens are indicated as “complete”.

The terminology and pattern of the descriptions follows Geiger (2012), who included a complete glossary of shell terminology. The term “sutsel” introduced by Geiger & Marshall (2012) refers to the portion of the base between the suture and the lower keel of the selenizone above it. Special attention is given to whether axial sculpture on the shoulder reaches the suture or stops short of it.

Scanning electron microscope (SEM) images were taken at the Centro de Microscopia Eletrônica, in Departamento de Invertebrados, Museu Nacional/UFRJ, and the Santa Barbara Museum of Natural History. Preparation of shells to SEM followed standard methodology (Geiger et al., 2007).

Abbreviations of cited repositories: BMSM – Bailey-Matthews Shell Museum, Sanibel, Florida, U.S.A.; CCS – Center for Coastal Studies, Texas A&M University, Corpus Christi, Texas, U.S.A.; FLMNH – Florida Museum of Natural History, Gainesville, Florida, U.S.A.; FMNH – Field Museum of Natural History, Chicago, Illinois, U.S.A.; HLC – Harry Lee Collection, Jacksonville, Florida, U.S.A.; IBUFRJ – Instituto de Biologia, Universidade Federal do Rio de Janeiro, Brazil; LACM – Natural History Museum of Los Angeles County, Malacology, Los Angeles, California, U.S.A.; MNRJ – Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil; MORG – Museu Oceanográfico/FURG (MORG), Rio Grande, Brazil; MZSP – Museu de Zoologia, Universidade de São Paulo, Brazil; NHMUK – The Natural History Museum, London, England, Great Britain; NMW – National Museum Wales, Cardiff, Great Britain; RMNH – National Museum of Natural History, Naturalis, Leiden, The Netherlands; SBMNH – Santa Barbara Museum of Natural History, Santa Barbara, California, U.S.A.; SGPIH – Collection [Sammlung] Geological-Paleontological Institute, University of Hamburg, Germany; UMMML – University of Miami Marine Laboratory, Rosenstiel School of Marine and Atmospheric Sciences, Florida, U.S.A.; USNM – United States National Museum, Smithsonian Institution, Washington, District of Columbia, U.S.A.



## RESULTS

Family Anatomidae McLean, 1989  
Genus *Anatoma* Woodward, 1859

## Type species

*Scissurella crispata* Fleming, 1828 (by monotypy: misidentified by Woodward, 1859: subsequent designation by Geiger, 2012: 733–734).

*Anatoma aedonia* (Watson, 1886)  
(Figs. 1–16)

*Scissurella aedonia* Watson, 1886: 114, pl. 8, fig. 3; Pilsbry, 1890: 56, pl. 65 [erroneously pl. 58 in text and pl. 68: Geiger, 2012], figs. 1–3; Lange de Morretes (1949: 55).

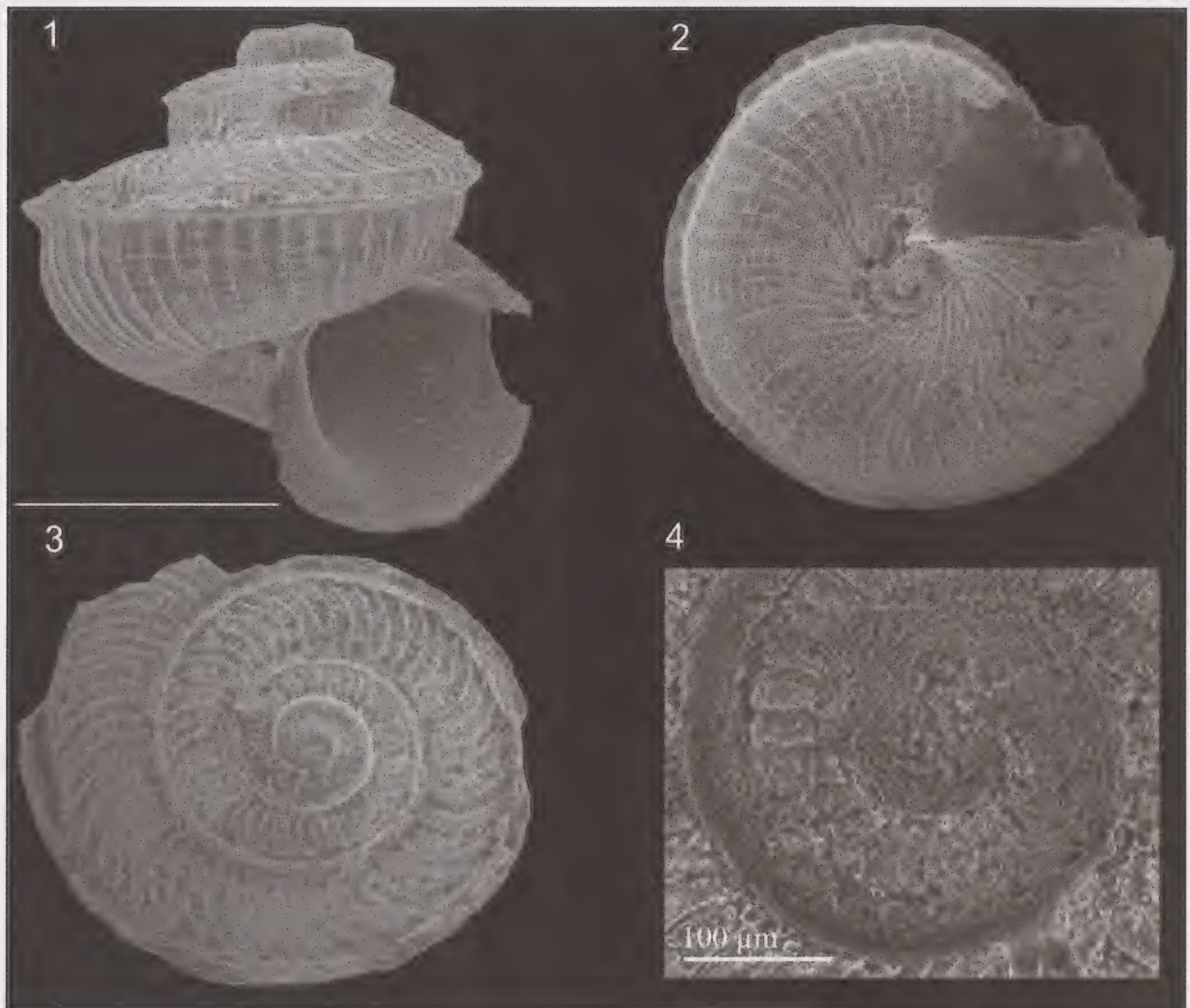
*Scissurella* (*Anatoma*) *aedonia*: Rios (1975: 12, pl. 1, fig. 8) [copy figure Watson, 1886].

*Anatoma aedonia*: Montouchet (1972: 10) [listed only]; Rios (1985: 10, pl. 5, fig. 34; 1994: 22, pl. 5, fig. 37; 2009: 24, text-fig.) [copy figure Watson, 1886]; Barros et al. (2001a: 62, fig. 2a); Barros et al. (2001b: 4, fig. 2b); Geiger et al., 2007: fig. 5C; Geiger (2012: 739, figs. 592–594).

*Anatoma* s.l. *aedonia*: Geiger (2003: 74, in a list of species).

## Misidentifications

Not *Anatoma aedonia* [mixed taxon concept: is *A. alternatisculpta*, *A. americana* and ***A. copiosa*** n. sp.]: Absalão (1989: 2, cited in a list of taxa); Absalão et al. (2006: 229, cited in a list of taxa); Absalão (2010: 91, cited in a list of taxa).



FIGS. 1–4. *Anatoma aedonia*. Lectotype designated by Geiger (2012). Scale bars: whole shells = 1 mm.

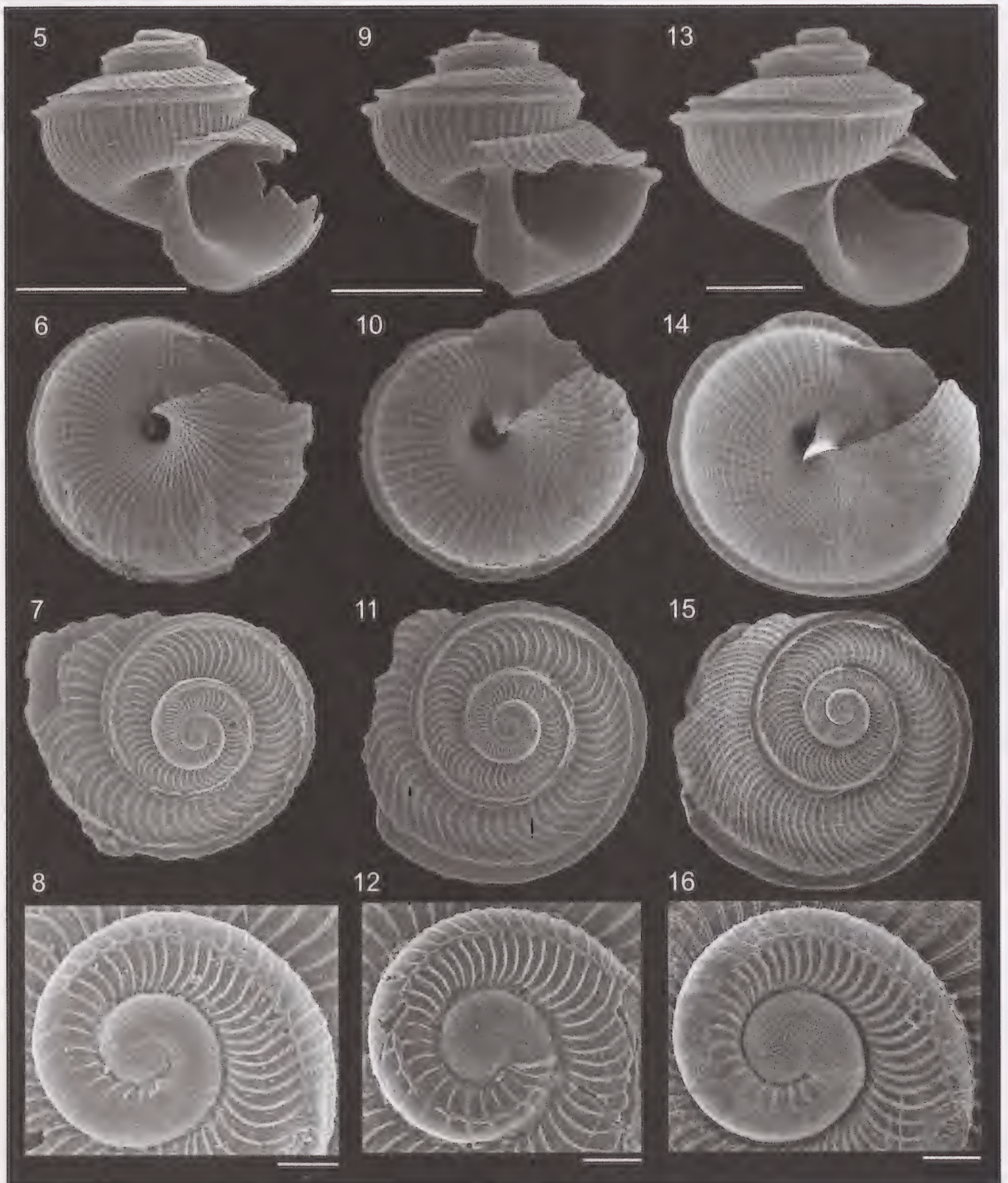


## Type Material

Lectotype: NMW 155.158.600 (subsequent designation by Geiger, 2012: 739, fig. 593C).

Paralectotypes: from type locality: NHMUK 1887.2.9.398–401 [4 shells, all but one

destroyed by Byne's/glass disease: Geiger et al., 2007: fig.5C]; RMNH [2]; NMW 155.158.600 [5]; from Station 135c, 100–155 fms. [= 183–274 m], Nightingale Island, Tristan de Cunha [St. Helena], 37°25'30"S, 12°28'30"W.



FIGS. 5–16. *Anatoma aedonia*. FIGS. 5–8: MNRJ 17280; FIGS. 9–12: MORG 49202; FIGS. 13–16: MNRJ 25954. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.



## Type Locality

Challenger station 122, 350 fms [= 640 m], off Pernambuco, Brazil (9°5'S, 34°50'W), restricted by Geiger (2012).

## Material Examined

The types; specimens cited in Geiger (2012) and: *Mexico*: Yucatan Channel (18.000°N, 457 m): USNM ex 780317, [8]; *Brazil*: São Pedro and São Paulo Archipelago (00°55'00"N, 29°20'42" ~ 8 m): MNRJ 17280, [2]; *off Pernambuco state*: (08°43.2'S, 35°03.7'W, 370 m): MNRJ 17287, [1]; ship Natureza coll., 18/xi/2000: MORG 49202, [1]; *off Bahia state*: continental slope of Abrolhos Archipelago: MD55 sta. 41–SY74 (18°58'S, 37°48'W, 682 m): MNHN, [2]; MNRJ 25953, [1]; MZSP 113476, [3]; MD55 sta. 42–CB76 (18°59'S, 37°50'W, 637 m): MNHN, [4]; MNRJ 25903, [3]; MZSP 118419, [2]; *off Rio de Janeiro state*: off Cabo Frio: MD55 sta. 65–CB105 (23°47'S, 42°10'W, 610 m): MNRJ 25954, [1]; Campos Basin: Oceanprof I sta. 74 (22°27'31"S, 40°09'23"W, 750 m), 21/xi/2002: MNRJ 26702, [1].

## Description

See Geiger (2012).

## Remarks

*Anatoma aedonia* (Figs. 1–16) was described by Watson (1886) based on few shells collected during the Challenger Expedition in deep water (640 m) off the coast of Pernambuco state, northeastern Brazil (type locality), and Tristan da Cunha Island, Santa Helena.

Subsequent records of this species from Brazil are problematic: those by Rios (1975, 1985, 1994, 2009) reproduced the original drawing, without adding new information; Barros et al. (2001a, 2001b) recorded the same specimen from the continental slope of Pernambuco state (1,713 m), but the illustration is very poor; the records by Absalão (1989), from Espírito Santo state, Absalão et al. (2006), from the central coast of Brazil, and Absalão (2010) from the Campos Basin, southeastern Brazil, contain neither illustration nor description and were based on misidentification of three other *Anatoma* species, including one new species here described (see discussions below).

Finally, Geiger (2012) redescribed the species based on type material, designated a lec-

totype (here figured in Figs. 1–4) and provided new records from the Caribbean region.

Almost all lots stored in Brazilian malacological collections here examined were originally determined as *A. aedonia*, but after a detailed examination, few are conspecific with the lectotype. The other lots contained any of the other species here studied.

Except for the record of the paralectotype from Tristan da Cunha in the South Atlantic, the few records of *A. aedonia* are restricted to localities above ~ 23°S latitude, from off Rio de Janeiro state, along the southeastern coast of Brazil, to off Pernambuco state and Arquipélago de São Pedro e São Paulo (northeastern coast), always deeper than 300 m. It is also known from several localities in the Caribbean and southern U.S.A. (Geiger, 2012). The deepest record by Barros (2001 a, b) of 1,713 m could not be checked by this revision.

## Distribution

U.S.A.: Florida; Gulf of Mexico; Caribbean; Brazil: Pernambuco to Rio de Janeiro states, São Pedro e São Paulo Archipelago; Tristan da Cunha; 183 m to 750 m.

*Anatoma proxima* (Dall, 1927)  
(Figs. 17–52)

*Scissurella proxima* Dall, 1927a: 110, not illustrated; Abbott, 1974: 17; Odé, 1986: 72.

*Scissurella proxima* new species [*sic*]: Dall, 1927b: 10.

*Anatoma proxima*: Bandel, 1998: 29, pl. 8, figs. 7–8, pl. 9, fig. 1, pl. 11, figs. 2–3; Geiger, 2003: 74, list of species; Geiger et al., 2007, fig. 7; Tunnell et al., 2010: 114, text-fig.; Geiger (2012: 1027, *partim*: figs. 835, 836C).

*Anatoma aedonia auct., non* Watson, 1886: Absalão et al. (2006: 229, *partim*) [in a list of taxa].

## Midentifications

Not *Anatoma proxima* (*partim*): Geiger, 2012: fig. 837A–B: is *A. americana*.

Not *Anatoma proxima* (*partim*): Geiger, 2012: fig. 836A–B: is *A. atlantica*.

Not *Anatoma proxima* (*partim*): Geiger, 2012: fig. 837C: is ***A. copiosa***, n. sp.

## Type Material

Holotype: lost before 1996 (Geiger, 2012 after study of USNM collection records): USNM



322962 off South Carolina, *Albatross* sta. 2314 (32.717°N, 77.850°W, 159 fms. = 291 m).

Neotype here designated (Figs. 17–20): USNM 449419.

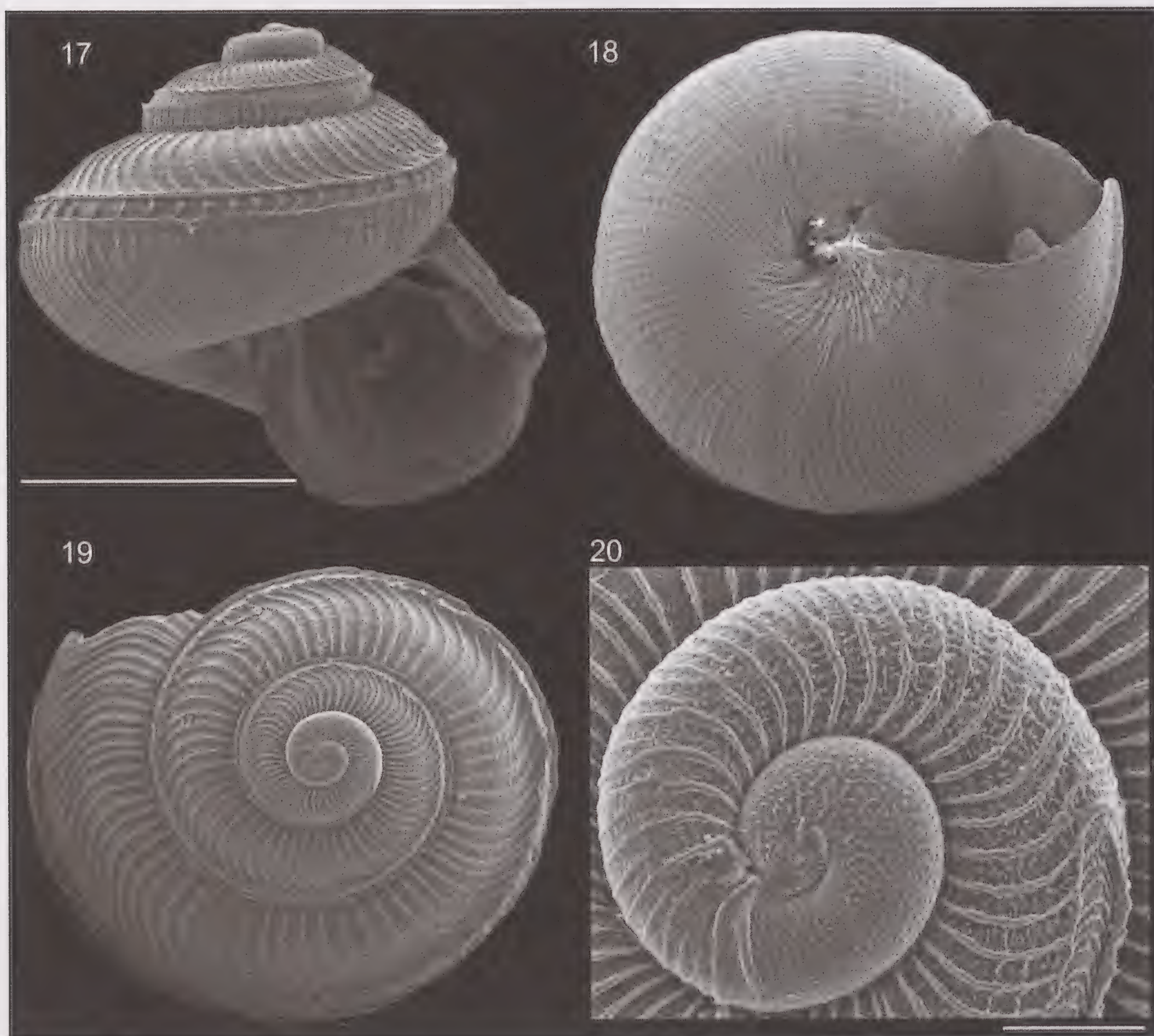
#### Type Locality

Biscayne Bay, Fowley Rocks Light, Florida, U.S.A. (25.583°N, 80.100°W, 146 m).

#### Material Examined

U.S.A.: *Virginia*: Chesapeake Bay (37.000°N, 76.000°W, 128 m): USNM 44536, [1]; USNM 322602, [1]; *South Carolina*: 3 off Charleston, (32.733°N 78.095°W, 213–223 m): USNM 875142, [8]; *Texas*: 222 km E of Corpus Cristi

(27.916°N, 94.817°W, 123 m): USNM 780315, [2]; *Florida*: Station 2662, off St. Augustine Harbor (~ 30.063°N, 79.640°W, 794 m): USNM 93353, [1]; off Caesars Creek (29.822°N, 84.993°W, 165 m): USNM 449423, [12]; W of Anna Maria, Manatee County (27.530°N, 82.734°W): BMSM 825, [1]; off Boynton, Palm Beach County (26.517°N, 80.067°W, 550 m): LACM 116022, [5]; off Boynton, Palm Beach (26.516°N, 80.067°W): FMNH 29982, [3]; off Del Ray, (26.450°N, 84.067°W, 320–366 m): FMNH 133207, [7]; Fowey Light (25.583°N, 80.100°W, 165 m): USNM 449418, [4]; Fowey Light (25.583°N, 80.100°W, 146 m): USNM 1282259 (ex 449419), [6]; off Fowey Light (25.583°N, 80.100°W, 128–165 m): USNM 449406, [2]; off Fowey Light (25.583°N, 80.100°W, 302 m):

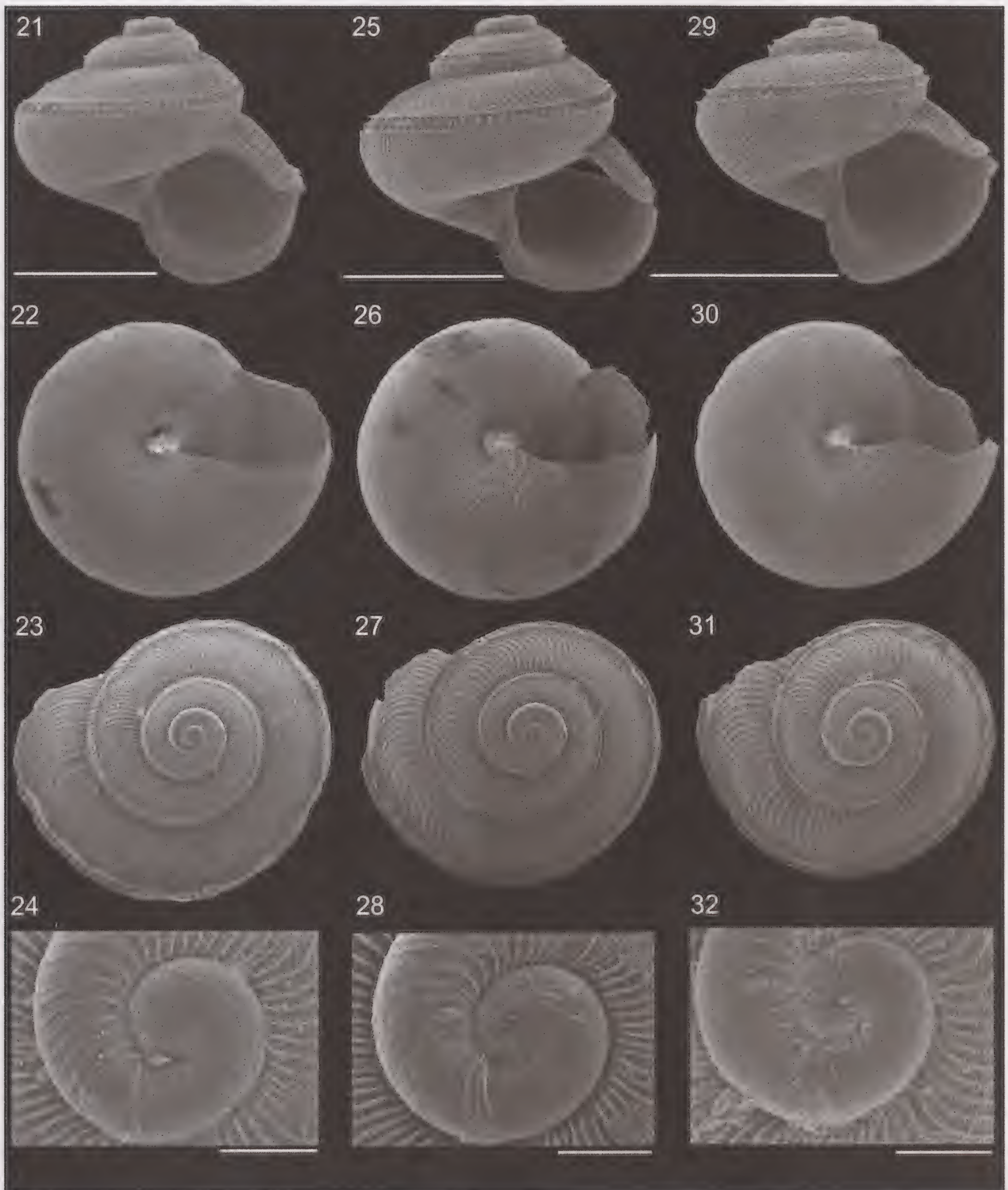


FIGS. 17–20. *Anatoma proxima*. Neotype here designated. Scale bars: whole shells = 1 mm, detail = 100  $\mu$ m.



USNM 449404, [1]; off Fowey Light (25.583°N, 80.100°W, 128–165 m): USNM 449406, [2]; off Fowey Light (25.583°N, 80.100°W, 183 m): USNM 449417, [1]; off Govt. cut, Miami (25.766°N, 80.183°W, 37 m): USNM 757602, [1]; Ragged Key (25.530°N, 80.172°W, 183 m):

USNM 449426, [5]; Triumph reef (25.486°N, 80.115°W, 128–165 m): USNM 450581, [3]; 50 miles W of Dry Tortugas (24.650°N, 83.533°W, 201 m): UMML 30.12031, [1]; 205° off Sombrero Light, Monroe County (24.600°N, 81.100°W, 183–201 m): FLMNH 249525, [5];



FIGS. 21–32. *Anatoma proxima*. FIGS. 21–24: FLMNH 249525; FIGS. 25–28: FMNH 29982; FIGS. 29–32: USNM 450581. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.



off Key West, (24.555°N, 81.783°W, 165 m): USNM 449414, [2]; Sand Key (155 m, ambiguous locality name): USNM 449422, [1]; off Sand Key (210 m, ambiguous locality name): USNM 449402, [1]; off Sand Key (128 m, ambiguous locality name): USNM 449421, [2]; off Florida Keys, T. McGuinty leg.: MORG 36799, [2]; off Western Dry Rocks (24.445°N, 81.928°W, 165 m): USNM 449413, [1]; Fowey Light, (25.583°N 80.100°W, 201 m): USNM 449420, [1]; off Boynton (26.525°N, 80.067°W, 503 m): USNM 889877, [1]; off Fernandina (30.669°N, 81.463°W, 538 m): USNM 87360, [1].

*Gulf of Mexico*: NW Gulf of Mexico: USNM 780316, [1]; *Barbados*: off Pelican Island (13.166°N, 59.567°W, 229 m): USNM 500688, [1].

*Brazil*: off *Amapá state*: (04°27'54"N, 049°58'05"W, 160 m), 13/x/2000, P. M. S. Costa leg.: MNRJ 26612, [1]; off *Pernambuco state*: (08°47.5'S, 34°46.6'W, 690 m): MNRJ 17078, [2]; (08°43.2'S, 35°03.7'W, 370 m): MNRJ 17288 [1]; (625 m), *Natureza* coll.: MORG 50753, [1]; (690 m): MORG 50051, [1]; (480 m), Oceanographic Ship *Antares* coll., 30/i/2001: MORG 49353, [1]; off *Espírito Santo state*: REVIZEE Central sta. C5-17 (18°34'S, 38°04'W, 65 m), 29/vi/2001: IBUFRJ 18797, [1]; REVIZEE Central sta. C5-25A (19°33'S, 38°45'W, 230 m), 28/vi/2001: IBUFRJ 13727, [2]; IBUFRJ 18789, [2]; East of Rio Doce's outfall, MD55 sta. 53-CB 92 (19°34'S, 38°55'W, 340-360 m): MNHN, [1]; *Campos Basin*: (21°58'S, 40°02'W, 142 m), 18/vi/2005: MZSP 93388, [3]; MZSP 113464, [2]; HAB 11 sta. E-05 (22°23'34.7"S, 40°20'47.3"W, 152 m), 23/iii/2009: MNRJ 16433, [1]; HAB 11 sta. A-05 (23°36'10.3"S, 41°21'36.1"W, 142 m), 01/iii/2009: MNRJ 17001, [1]; MNRJ 16435, [1]; SBMNH 230142, [2]; x/2008, P. M.S. Costa leg.: MNRJ 17260, [6]; SBMNH 230141, [4]; MNRJ 17261, [8]; off *São Paulo state*: (24°40'S, 44°52'W, 134 m), 08.v.1970: MZSP 43034, [9]; MZSP 35070, [8, complete]; MZSP 54615, [11]; MZSP 35061, [34]; MZSP 35067, [13]; MZSP 35063, [7]; off *Rio Grande do Sul state*: REVIZEE Sul sta. 6757 (30°09'S, 48°17'W, 242 m), 16/iv/1998: Oceanographic Ship *Antares* col.: MORG 43220, [2]; off Porto Alegre (30.716°S, 49.083°W, 224 m): HLC, [1]; REVIZEE Sul sta. 6851 (31°57'S, 50°09'W, 160 m), 06/iv/1998, Oceanographic Ship *Antares* col.: MORG 42282, [1].

Material Examined of *Anatoma* cf. *proxima* (spiky form): U.S.A.: *Gulf of Mexico*: Johns Pass (27.534°N, 84.169°W, 62 m): FLMNH

ex 233961, [1]; off *Louisiana*: (28.008°N, 91.238°W): CCSC, [1]; *Florida*: off Sambo Reef, Monroe County (24.500°N, 81.667°W, 120 m): FLMNH 155183, [1]; *Mexico*: off Cozumel (20.950°N, 86.567°W, 120 m): UMML 30.12047, [1]; *Barbados*: off Pelican Island (13.166°N, 59.567°W, 268 m): USNM 500677, [3]; off Pelican Island (13.166°N, 59.567°W, 137 m): USNM 500695, [1]; off Pelican Island (13.166°N, 59.567°W, 137-146 m): USNM 500678, [1].

#### Redescription

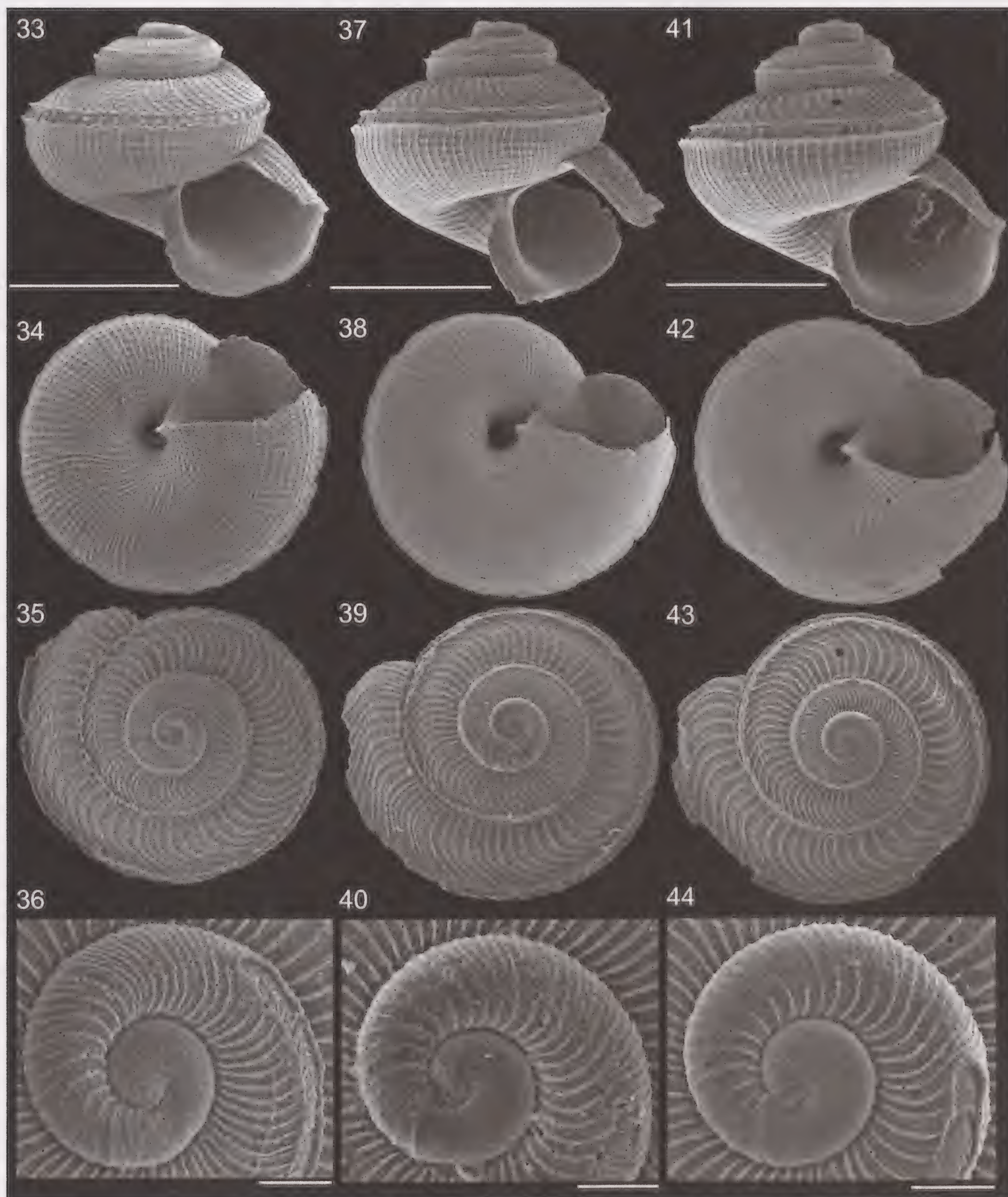
Shell trochiform, spire slightly turreted, 1.75 mm high, 1.92 mm wide (neotype). Protoconch of ~ 0.8 whorl, with dense flocculent sculpture, faint apertural varix, not connected to embryonic cap; apertural margin straight. Teleoconch I of ~ 0.6 whorl, with ~ 40 axial ribs, some reaching upper suture, some stopping short of it, intercalated and sometimes merging in pairs; interstices irregularly granulated, ~ 2x as wide as ribs at onset of teleoconch I, becoming narrower (as wide as ribs) towards onset of selenizone; without spiral cord. Teleoconch II up to 2.5 whorls, suture strongly impressed; shoulder profile straight to somewhat convex, with ~ 55 to ~ 90 axial ribs on second whorl (89 in neotype) extending onto keel of selenizone; in few shells, some axial ribs not reaching suture, irregularly distributed, and with slight crisp elevation close to suture; interspaces about as wide as cords at suture, twice as wide near selenizone; interspaces becoming wider with growth; spiral lines about a quarter as strong as axial ribs, running over them, forming slightly elevated thickenings; first spiral line at onset of selenizone, 6-8 on second whorl, 10-12 at apertural margin. Sutsel high, ~ 2x width of selenizone at first whorl of teleoconch II. Base with very faint constriction below selenizone, profile rounded; ~ 80-100 axial ribs as strong as on shoulder, reaching edge of selenizone, sometimes becoming evanescent towards aperture, interspaces as wide as ribs; ~ 20 spiral cords, irregularly spaced, thicker in umbilical region, running over axial ribs, forming very slight thickening at intersections. Umbilicus of moderately width; funiculus present. Aperture rounded, adumbilical portion slightly flared. Selenizone at periphery, moderately wide; keels very short; lunules distinct, not aligned to axial ribs.

Jaw (Figs. 45-49). Triangular, composed of rhomboidal elements.



Radula (Figs. 50–51). Rachidian tooth trapezoidal, base about twice as wide as tip; central cusp short, slightly larger than lateral cusps, cusps arranged in row parallel with row of teeth; 5–6 lateral cusps on each side. Lateral teeth similar, elongating from lateral

tooth 1 to larger, sickle-shaped lateral tooth 5, 2x for overall tooth, 3–4x for tip; elongated, with acuminate tip, ending in sharp, pointed central cusp; three smaller cusps on each side of lateral teeth 1–4; 5–6 smaller cusps on each side of lateral tooth 5. Inner marginal elongated, with



FIGS. 33–44. *Anatoma proxima* from Brazil. FIGS. 33–36: MNRJ 16435; FIGS. 37–40: MNRJ 17001; FIGS. 41–44: MNRJ 17261. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.

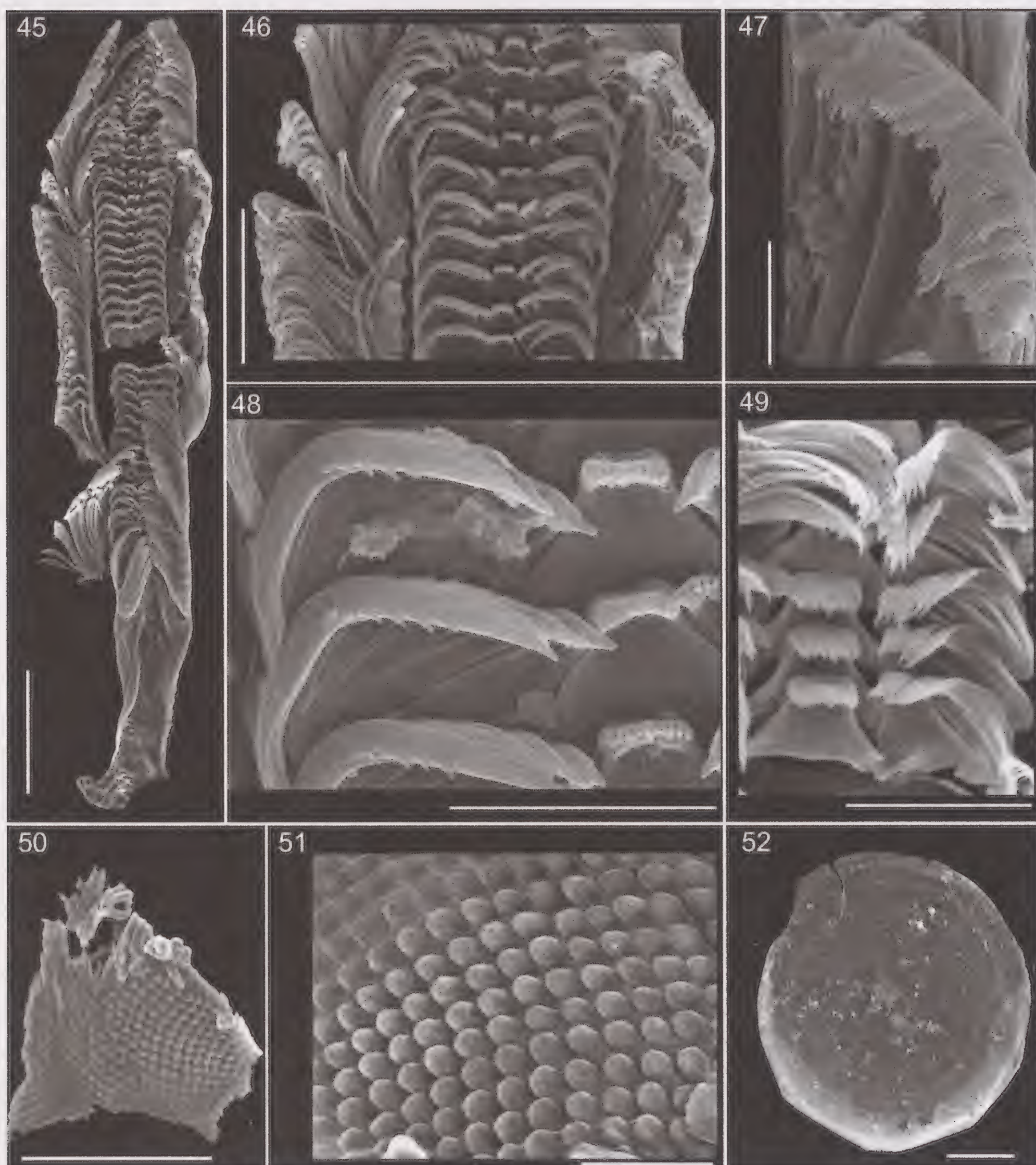


terminal pointed tip, ~ 20 smaller cusps along edge; shafts without food groove. Middle marginal teeth elongated with decreasing number of finer cusps along edge of tip. Outermost marginal teeth paddle-shaped, with approximately 5–8 fine bristles on each side of tip. Radular interlock of central field moderate.

Operculum (Fig. 52). Thin, corneous, multi-spiral, with central nucleus.

#### Remarks

As discussed by Geiger (2012), *Anatoma proxima* was described twice (Dall, 1927a, b),



FIGS. 45–52. *Anatoma proxima*. FIGS. 45–48: USNM 44536; FIGS. 49–52: MZSP 35070. FIG. 45: Entire radula; FIG. 46: Central field; FIG. 47: Outer marginal teeth; FIGS. 48, 49: Central field enlarged; FIG. 50: Jaw; FIG. 51: Detail of jaw elements; FIG. 52: Operculum. Scale bars: FIGS. 45, 50 = 100  $\mu$ m; FIG. 46 = 50  $\mu$ m; FIG. 47 = 10  $\mu$ m; FIGS. 48, 49, 51 = 20  $\mu$ m; FIG. 52 = 200  $\mu$ m.



the latter publication being a *lapsus calami*. The original description with measurements (Dall, 1927a) was based on one shell from South Carolina, *Albatross* sta. 2314 (USNM 322962). This is the holotype, which has been lost prior to 1996.

Besides South Carolina, Dall (1927a: 110) mentioned that “the species has been collected in St. Augustine and numerous localities on the coasts off the keys of Florida”. Only USNM 93353, from 434 fms. [= 794 m], Stn. 2662, off St. Augustine Harbor [Florida, U.S.A., ~ 30.063°N, 79.640°W] matches the data of the original description, the remaining indications being too vague to permit identification of other types. Geiger (2012), thus, considered that this shell is a “probable paratype”: the locality data match and the specimen was collected prior to the description of the species, but the lot number was not referred to explicitly in the original description. However, USNM 93353 is a very damaged shell, with almost completely broken last whorl and fully eroded protoconch and teleoconch I, so that important characters to recognize the taxon are not visible.

Given that the identity of the name is controversial, as will be discussed below, and that the original type is no longer extant and other possible specimens examined by Dall (1927a) cannot be located, we designate here the shell USNM 449419 (Figs. 17–20), from south Florida, as the neotype of *Scissurella proxima*, with the explicit intent to stabilize the nomenclature of the taxon. It was collected in the region where Dall (1927) originally recorded the species.

Geiger (2012) considered *A. proxima* as a quite variable species, in shell shape and sculpture, synonymizing *Anatoma americana* Bandel, 1998, under it. The present study, based on several shells of *A. proxima* from Brazil, in addition to re-examination of material of this taxon from the U.S.A. and the Caribbean made it possible to reconsider the variability of the characters in *A. proxima*. The species is redescribed, restricting the taxon concept, and recognizing four different taxa among *A. proxima* sensu Geiger (2012).

*Anatoma proxima* (Figs. 17–44) can be characterized by a shell with moderately high sutsel and a rounded profile of the base (Figs. 17, 21, 25, 29, 33, 37, 41), a protoconch with densely flocculent sculpture and with a tiny spiral cord (Figs. 20, 24, 28, 32, 36, 40, 44), teleoconch I without spiral cord, and with axial ribs of shoulder alternatingly reaching suture or stopping short of it (Figs. 24, 28, 32, 36, 40, 44).

In a few shells of *A. proxima* some select axial ribs do not reach the suture on teleoconch II (Fig. 23), but it is not the regular pattern seen in *A. americana* (see below).

Among the illustrations by Geiger (2012) of *A. proxima*, only those in figures 835 and 836C are herein considered as true *A. proxima*. The shells in figures 837A and 837B in Geiger (2012) bear a regular pattern of alternating axial ribs reaching suture and stopping short of it over the shoulder of teleoconch II, as seen in the holotype of *A. americana*. Contrary to Geiger (2012), who considered it intraspecific variability due to limited material showing this pattern, we consider *A. americana* a valid name based on consistent patterns in more numerous specimens. A more detailed comparison is presented below, in the remarks of *A. americana*.

The specimens figured by Geiger (2012: fig. 836A–B, also radula fig. 838) from Florida are here re-identified as *A. atlantica*; his figure 837C, from Brazil, is *Anatoma copiosa*, n. sp. All those shells have a conical, not turreted spire, low sutsel, less rounded base profile, a more angulated last whorl, and denser spiral sculpture on the shoulder.

The radula of the true *A. proxima*, based on specimens from Virginia, U.S.A. (USNM 44536) (Figs. 45–47) and from Brazil (MZSP 35070) (Figs. 48, 49), has a rachidian tooth with all cusps of approximately equal size (Figs. 46, 48, 49) and a lateral tooth 4 that is not reduced in size. Both those characters are uncommon in *Anatoma*.

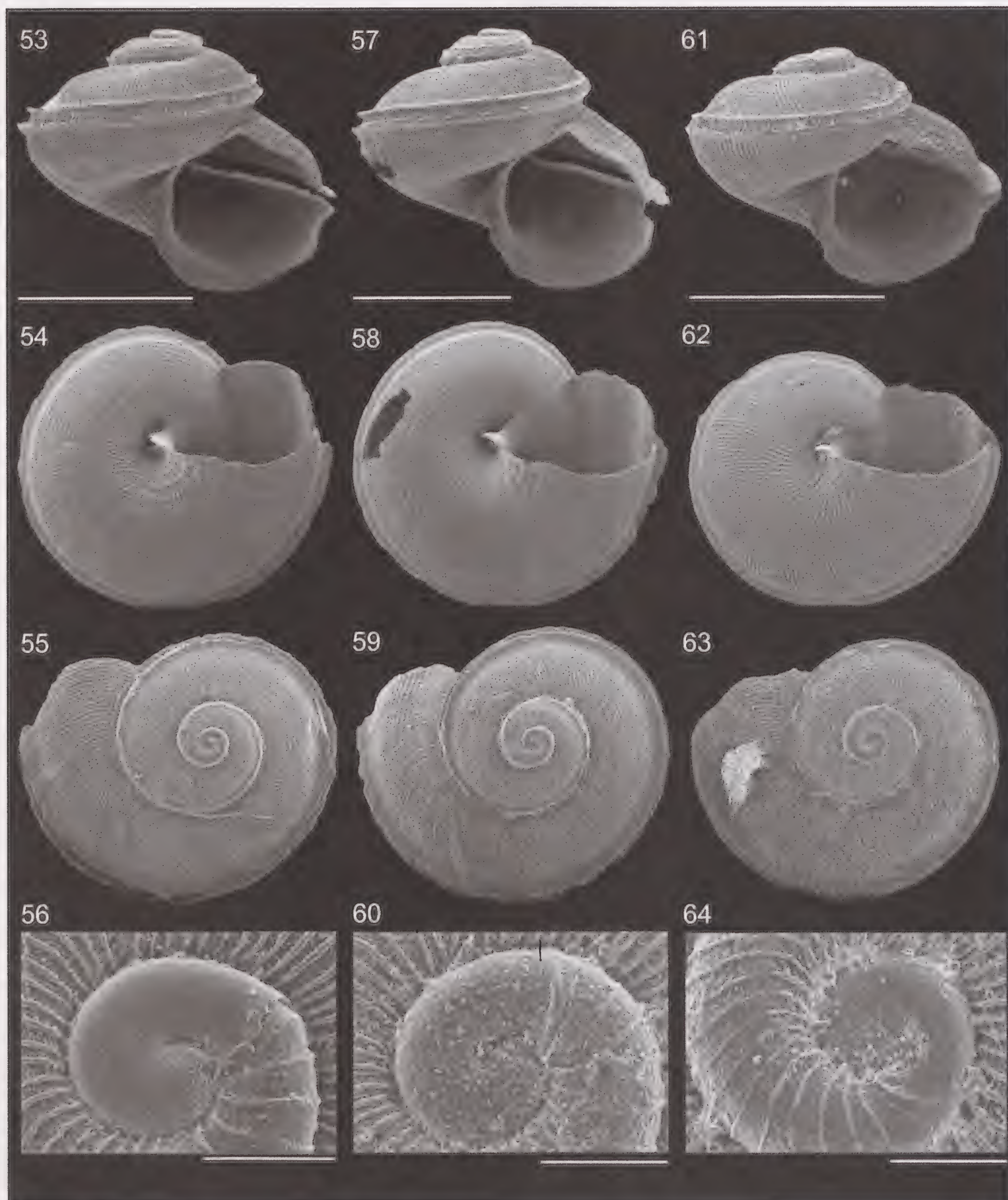
Geiger (2012: p. 1034) discussed some intraspecific variability with respect to the spiral cord in position of the selenizone on teleoconch I. Specimens from Brazil were noted as having it, while those from the Caribbean and the U.S.A. lack it. This character can exhibit some true intraspecific variability as in *A. atlantica* (see below), but *A. proxima* in the more narrow sense discussed here never has it. In that context, Geiger (2012: 1034) referred to the illustration in Leal (1991), but that shell is recognized here as the more lenticular, southern form of *A. alternatisculpta* (see discussion below).

*Anatoma proxima* (Figs. 17–44) is very similar in shell shape and overall sculpture to *Anatoma aedonia* (Figs. 1–3, 5–7); both have a turreted spire and less discoid shape with very similar sculpture on teleoconch II. However, the number of axial ribs and spiral cords is much higher in *A. proxima*. The most important difference is the sculpture on teleoconch I: while *A. aedonia* has



a strong spiral cord in the position of the selenizone crossing the axial ribs, *A. proxima* lacks a spiral cord and the axial ribs alternate between reaching the suture and stopping short at around the middle of whorl height (Figs. 20, 24, 28, 32,

36, 40, 44). Besides that, the surface of the shell on teleoconch I in *A. proxima* is covered by numerous granules of irregular shape and spacing (Figs. 20, 24, 28, 32, 36, 40, 44), while in *A. aedonia* it is smooth (Figs. 8, 12, 16).



FIGS. 53–64: *Anatoma* cf. *proxima*. FIGS. 53–56: USNM 500677; FIGS. 57–60: USNM 500695; FIGS. 61–64: FLMNH ex 233961. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.



*Anatoma proxima* has a wide geographic distribution in the western Atlantic, from South Carolina to Rio Grande do Sul, Brazil, including the Gulf of Mexico and Barbados. In northeastern Brazil (off Pernambuco state), and is sympatric with *A. aedonia*, with same bathymetry. The shells from localities along the Brazilian coast (Figs. 33–44) show the same sculpture type but less dense than in the neotype (Figs. 17–20) and the remaining shells from northern localities (Figs. 21–32).

A few specimens of *Anatoma* cf. *proxima* (Figs. 53–64) have more pronounced nodular thickenings at the intersection of axials and spirals on shoulder, which are elevated into short spikes. Otherwise, those specimens share the smooth to flocculent protoconch sculpture, the rather weak apertural varix of the protoconch, the 0.66–0.75 teleoconch I whorls, the absence of a spiral in position of the selenizone on teleoconch I, and the overall density and strength of the teleoconch sculpture. At present, they are only known from the Caribbean. Figures 53–64 show three examples of this consistent form. However, we do not consider those specimens sufficiently distinct to warrant description of a new species.

#### Distribution

U.S.A.: South Carolina to Florida; Gulf of Mexico; Caribbean; Brazil: Pernambuco to Rio Grande do Sul states; 65 m to 794 m.

*Anatoma americana* Bandel, 1998  
(Figs. 65–76)

*Anatoma americana* Bandel, 1998: 29, pl. 8, figs. 4, 5.

*Anatoma aedonia* auctt., non Watson, 1886: Absalão (1989: 2, *partim*); Absalão et al. (2006, in part.: 229) [list of taxa].

*Anatoma proxima* auctt., non Dall, 1927: Geiger (2012, *partim*: figs. 837A, B).

#### Type Material

Holotype: SGPIH 3885, not located (Ulrich Kotthoff, pers. comm.).

#### Type Locality

Cape Lookout, North Carolina, U.S.A. (34.583°N, 76.533°W, 150 m) (original designation).

#### Material Examined

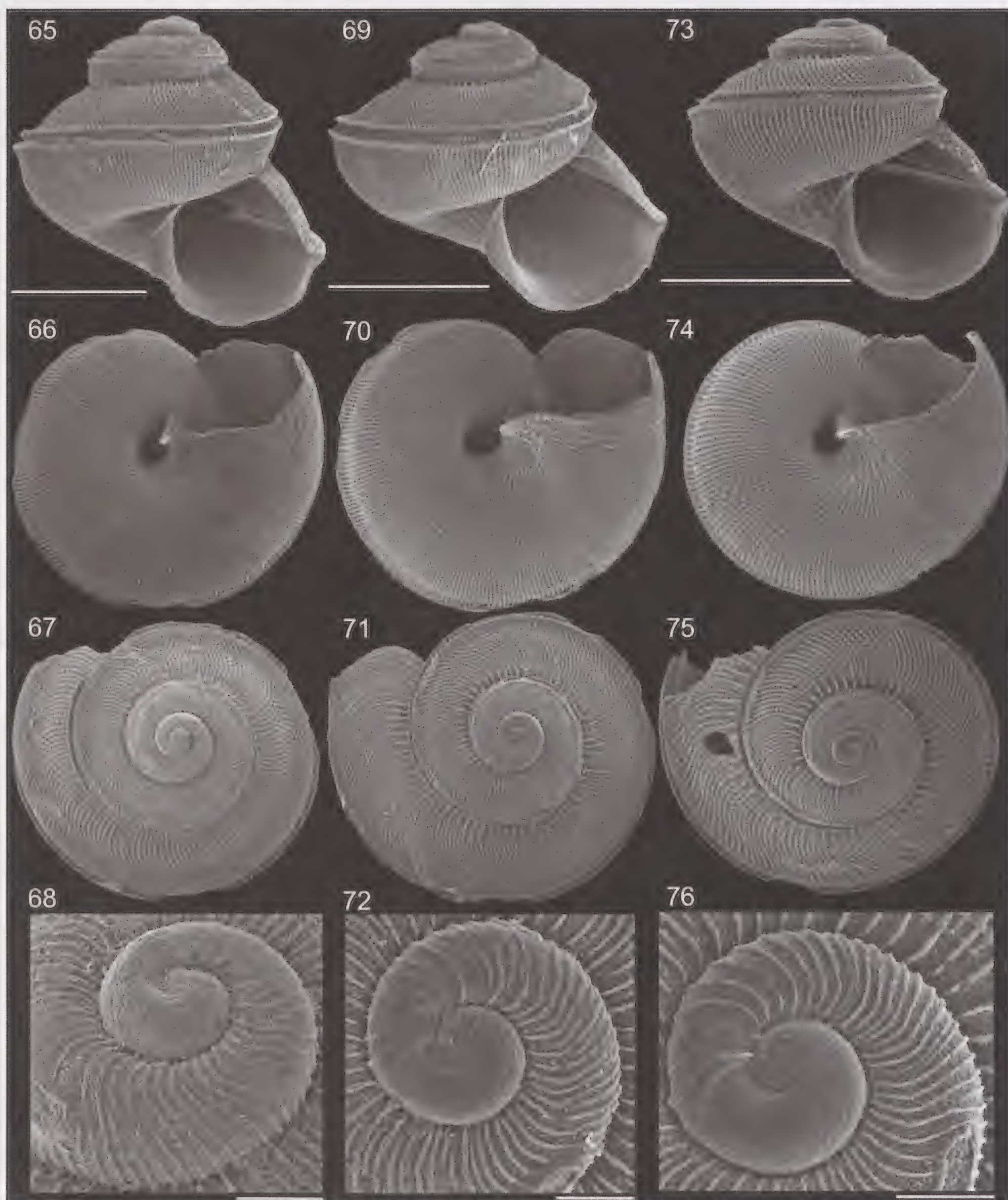
U.S.A.: *Alabama*: (29.583°N, 87.333°W): UMML 30.12034, [3]; *Mexico*: Yucatan Channel (18.700°N, 83.700°W, 457 m): USNM 780317, [2].

*Brazil*: off *Amapá* state: (04°27'54"N, 49°58'05"W, 160 m), 13/x/2000, P. M. S. Costa leg.: MNRJ 26611, [12]; *Abrolhos Archipelago*, continental slope: MD55 sta. 43–CB 77 (19°40'06"S, 37°48'01"W, 790–940 m): MNHN, [1]; off *Espírito Santo* state: 16/viii/1984, Oceanographic Ship *Almirante Saldanha* col.: IBUFRJ 1720, [3]; *Campos Basin*: HAB 13 sta. I–04 (21°22'55.2"S, 40°15'31.5"W, 103 m), 06/iii/2009: MNRJ 29794, [4]; HAB 13 sta. H–05 (21°42'33"S, 40°09'05.9"W, 147 m), 09/iii/2009: MNRJ 18172, [5]; HAB 11 sta. G–03 (22°03'41.2"S, 40°10'5.38"W, 75 m), 25/ii/2009: MNRJ 29798, [1]; HAB 11 sta. G–04 (22°04'10"S, 40°7'5.80"W, 92 m), 25/ii/2009: MNRJ 29797, [1]; HAB 16 sta. G–05 (22°06'06.1"S, 40°03'12.8"W, 149 m), 07/vii/2009: MNRJ 16438, [12]; HAB 11 sta. G–05 (22°06'06.2"S, 40°03'12.6"W, 154 m), 24/ii/2009: MNRJ 29796, [4]; HAB 11 sta. F–04 (22°12'33"S, 40°13'24.9"W, 100 m), 24/ii/2009: MNRJ 29791, [1]; HAB 11 sta. E–04 (22°17'37.7"S, 40°27'06"W, 103 m), 23/ii/2009: MNRJ 29789, [1]; HAB 13 sta. D–03 (22°19'27.6"S, 40°37'25.1"W, 75 m), 15/iii/2009: MNRJ 16441, [3]; MNRJ 29793 [1]; HAB 17 sta. D–04 (22°23'17.7"S, 40°35'05.2"W, 110 m), 25/vii/2009: MNRJ 16442, [8]; HAB 11 sta. E–05 (22°23'34.7"S, 40°20'47.3"W, 152 m), 23/iii/2009: MNRJ 29790, [2]; MNRJ 16427 [1]; HAB 11 sta. D–05 (22°31'02.8"S, 40°31'38.6"W, 139 m), 22/ii/2009: MNRJ 29792, [7]; (22°42'S, 40°40', ~ 110 m), 19/ix/2003: MNRJ 17223, [3]; (22°42'S, 40°40', ~ 110 m), 2007: MNRJ 17276, [10]; MNRJ 17071, [19]; SBMNH 230140, [10]; HAB 11 sta. C–03 (22°46'50.5"S, 41°03'39"W, 77 m), 22/ii/2009: MNRJ 16453, [1]; REVIZEE Central sta. C1–D1–2 (22°49'4.8"S, 41°9'25", 69 m), 23/ii/1996: IBUFRJ 11418, [5]; MNRJ 15674, [5]; MORG 40879, [11]; HAB 16 sta. C–04 (22°51'57.5"S, 40°57'34.8"W, 90 m), 03/vii/2009: MNRJ 16440, [3]; HAB 11 sta. C–04 (22°51'57.5"S, 40°57'35.1"W, 92 m), 22/ii/2009: MNRJ 29787, [1]; REVIZEE Central sta. C1–D3 (22°52'S, 41°09'W, 80 m), 23/ii/1996: IBUFRJ 11315, [6]; HAB 11 sta. C–05 (22°57'23.9", 40°50'36.4"W, 142 m), 21/ii/2009: MNRJ 29785, [4]; SBMNH 230139, [2]; (23°05'22.73"S, 40°58'55.52", ~ 100 m), 17/ix/2004: MNRJ 17224, [1]; HAB 16 sta.



B-04 (23°10'0.72"S, 41°3'12.5"W, 107 m), 02/vii/2009: MNRJ 16439, [8]; HAB 11 sta. B-05 (23°11'25.8"S, 41°0'54.0"W, 150 m), 21/ii/2009: MNRJ 29800, [1]; HAB 11 sta. A-05 (23°36'10.3"S, 41°21'36.1"W, 142 m), 01/iii/2009: MNRJ 29788, [12]; iv/1998, sup-

ply boat *Astro Garoupa* coll.: IBUFRJ 18887, [1]; 20-27/i/1998, supply boat *Astro Garoupa* coll.: IBUFRJ 19436, [22]; 2003, P.M.S. Costa leg.: MORG 48156, [3]; off São Paulo state: (24°40'S, 44°52'W, 134 m), 08.v.1970: MZSP 113475, [1]; MZSP 113469, [1].



FIGS. 65–76. *Anatoma americana*. FIGS. 65–68: MNRJ 29788; FIGS. 69–72: MNRJ 29788; FIGS. 73–76: MNRJ 29790. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.



## Description

Shell trochiform to lenticular, spire slightly turreted, up to 2.3 mm tall, 2.3 mm wide. Protoconch of ~ 0.8 whorl, with dense flocculent sculpture, spirally arranged line of granules at mid-line; apertural varix faint, not connected to embryonic cap, somewhat convex apertural margin. Teleoconch I of ~ 0.5 whorl, with ~ 30 axial cords, some not reaching upper suture; interstices approximately three times width of cords, covered by irregular granules; without spiral cord. Teleoconch II up to 2.75 whorls, suture strongly impressed; shoulder profile straight, with ~ 120 axial ribs on second whorl, in an alternating pattern of reaching suture and stopping short of it, sometimes merging close to suture, extending onto keel of selenizone; in some large specimens all axial ribs close to apertural margin reaching suture; interspaces as wide as cords; spiral lines about half as strong as axial ribs, running over axial ribs, forming slight thickenings at intersections, first spiral line at onset of teleoconch II, increasing in number to ~ 15 at shoulder of second whorl. Sutsel increasing in width with growth, from half as wide as selenizone at onset of selenizone to ~ 3x width of selenizone at apertural margin. Base with faint constriction below selenizone, profile slightly rounded, ~ 140 axial ribs as strong as on shoulder, very closely spaced, reaching edge of keel of selenizone; about ~ 25 fine spiral cords irregularly spaced, not reaching keels of selenizone, running over axial ribs, forming slight thickenings at intersections. Umbilicus of moderate width; funiculus present. Aperture rounded, adumbilical portion slightly flared. Selenizone at periphery, moderately wide; lunules moderately strong, regularly spaced, somewhat aligned to axial ribs; keels of moderate strength and elevation, abapical keel more developed. Animal unknown.

## Remarks

The description presented above was based mainly on the material from Brazil, with the addition of some shells from the U.S.A. and Mexico [considered by Geiger (2012) as a variation of *A. proxima*]. The holotype itself could not be examined, because it is missing from the shelf at the originally cited repository in SGPIH (Ulrich Kotthoff, pers. comm.).

The material here studied agrees with the original figure of the holotype (Bandel, 1998: pl. 8, figs. 4, 5). The only difference to the

original illustrations (Bandel, 1998: pl. 8, fig. 6) is the absence, in all shells here examined, of a spiral cord in teleoconch I (Figs. 68, 72, 76); this spiral cord is not mentioned in the original description. However, this figure (Bandel, 1998: pl. 8, fig. 6) is not a detail of the holotype, but of another shell, from Florida (while the holotype is from North Carolina). Geiger (2012: fig. 834) reproduced the three original figures and erroneously indicated all three as the holotype of *A. americana* (Geiger, 2012: 1027).

A carefully comparison of this figure (Bandel, 1998: pl. 8, fig. 6) to the apical view of the holotype in Bandel (1998: pl. 8, fig. 5) revealed that the sculpture is quite different: the holotype lacks a spiral cord and the axial cords alternately reach suture and stop short of it in teleoconch I, while the specimen in fig. 6 has a spiral cord in the position of the selenizone and all axial cords reach the suture. Thus, the shell in figure 6 of Bandel (1998) is not conspecific with the holotype. Unfortunately, the material studied by Bandel (1998) was not found and could not be further examined. Given the limited information on the shell, we are unable to correct the identification.

The shell from Florida in Bandel (1998: pl. 8, fig. 6) is a paratype (although not explicitly designated as such; ICZN Code Art. 72.4.1). Bandel (1998: 29) referred to additional material that he identified as *A. americana*, which all can be considered paratypes: "...further shells come from the shelf break off Florida from in between 50 and 200 m deep water of the Atlantic. ... the species ..., which can be proven to exist off the coast off Florida to Maryland from sediment samples on the shelf and the continental slope. [translated from German original]" The lack of specificity precludes us from providing a detailed discussion. Specimens may eventually be recognized as paratypes based on label annotations.

*Anatoma americana* (Figs. 65–76) can be easily distinguished from all other western Atlantic species by the presence of two types of axial ribs over shoulder of teleoconch II: some extending from the keel of selenizone and reaching the suture; the others that do not reach the suture. These two types of axial ribs are intercalated from about the onset of teleoconch II (Figs. 65, 71, 75); in some large specimens, all axial ribs extend to the suture on the final quarter whorl (Fig. 67). The ribs reaching the suture have a crisp elevated projection very close to the suture (Fig. 69). These projections in conjunction with the termination



of the axial ribs not reaching the suture form a spiral band about one tenth of the width of the shoulder away from the suture (Figs. 65, 71, 75). In addition, the sculpture on the base is much stronger and the ribs are more closely spaced in *A. americana* (Figs. 66, 70, 74).

Sculpture with axial ribs on the shoulder of unequal length is uncommon in *Anatoma* species. It is known from *Anatoma auporia* (Powell, 1937) from New Zealand, *Anatoma janusa* Geiger, 2012, from the tropical and subtropical northeastern Atlantic, *Anatoma parageia* Geiger & Sasaki, 2009, from Japan, *Anatoma philippinica* (Bandel, 1998), from Indo-Malayan Archipelago, and *Anatoma pseudoequatoria* (Kay, 1979) from the Indo-Malayan Archipelago to the Central Pacific.

As discussed above, Geiger (2012) considered *Anatoma proxima* with a wide intraspecific variation, which would encompass *A. americana*, and proposed the synonymy between these two names. However, in *A. americana*, the pattern of two types of axial ribs on teleoconch II is a rather constant characteristic, while in *A. proxima*, most of the shells have all axial ribs extending to the suture (Figs. 27, 31, 35, 39, 43–19), including the here designated neotype (Fig. 19). In some shells of *A. proxima* from the U.S.A. and the Caribbean, some short ribs can be found, but in a very irregular pattern (Fig. 23). This difference is more evident when the shells are observed in apical view.

#### Distribution

U.S.A.: North Carolina, Alabama; Mexico: Yucatan Channel; Brazil: Amapá state, Abrolhos Archipelago, Espírito Santo to São Paulo states); 69 m to 940 m.

*Anatoma atlantica* (Bandel, 1998)  
(Figs. 77–94)

*Hainella atlantica* Bandel, 1998: 38–39, pl. 13, figs. 1–3.

*Anatoma atlantica*: Geiger (2012: 788, figs. 633–635).

*Anatoma proxima* auctt., non Dall, 1927: Geiger (2012, partim.: figs. 836A, B, 838).

*Anatoma* cf. *crispata*: Tunnell et al., 2010: figs. 3.30-5-5a, 114, text-fig.

#### Type Material

SGPIH 3877, not located (Ulrich Kotthoff, pers. comm.).

#### Type Locality

Off southern Florida, U.S.A. (200 m) (original designation).

#### Material Examined

U.S.A.: *Louisiana*: (27.873°N, 91.848°W): CCSC, [4]; *South Carolina*: off Charleston (32.738°N, 75.089°W, 223–233 m): USNM 875208, [7]; (32.733°N, 78.095°W, 213–223 m): USNM 1233936 (ex 875142), [6]; *Florida*: off Fernandina (30.669°N, 81.463°W, 538 m): USNM ex 108147, [1]; 170° off Sombrero Light, Monroe County (24.610°N, 81.100°, 128–137 m): FLMNH 249924, [1]; off Sambo Reef (24.500°N, 81.717°W, 210 m): USNM 449412: [7]; off Sambo Reef (24.499°N, 81.645°W, 216 m): USNM 449411, [5]; off Sambo Reef (Eolis sta. 329, 247 m): USNM 449409, [15]; off Sambo Reef (24.500°N, 81.667°W, 219 m): USNM 449410, [13]; Sand Key, Sand Keys, Biscayne Bay, (25.500°N, 80.030°W, 165 m): USNM 449408, [1]; 219 m, off Sand Key, Sand Keys, Biscayne Bay (25.500°N, 80.030°W): USNM 449403, [3]; Key West, (24.555°N, 81.783°W, 137–146 m): USNM 449416, [1]; off Key West (24.554°N, 81.792°W, 201 m): USNM 449415, [6]. *Mexico*: off Cozumel (20.916°N, 86.467°W, 198 m): UMML 30.12045, [2]; *Barbados*: (13.167°N, 59.567°W): USNM 126817, [1]; off Pelican Island, 13.167°N, 59.567°W, 60 m): USNM 500679, [1]; off Pelican Island, (13.166°N, 59.567°W, 229): USNM 500688, [1].

*Brazil*: off Amapá state: MNRJ 26613, (04°27'54"N, 49°58'05"W, 160 m), 13/x/2000, P. M. S. Costa leg. [63]; SBMNH 452776, [4]; off Pernambuco state: (8.700°S, 34.200°W, 600 m): DLG 1208, [2]; Abrolhos Archipelago, continental slope: MD55 sta. 40–DC 72 (19°S, 37°49'W, 950–1,050 m): MNHN, [1]; MD55 sta. 43–CB 77 (19°41'S, 37°48'W, 790–940 m): MNHN, [11]; off Rio de Janeiro state: Campos Basin: (21°58'S, 40°02'W, 142 m), 18/vi/2005: MZSP 113463 [2]; x/2001, P.M.S. Costa leg.: MNRJ 25620, [5].

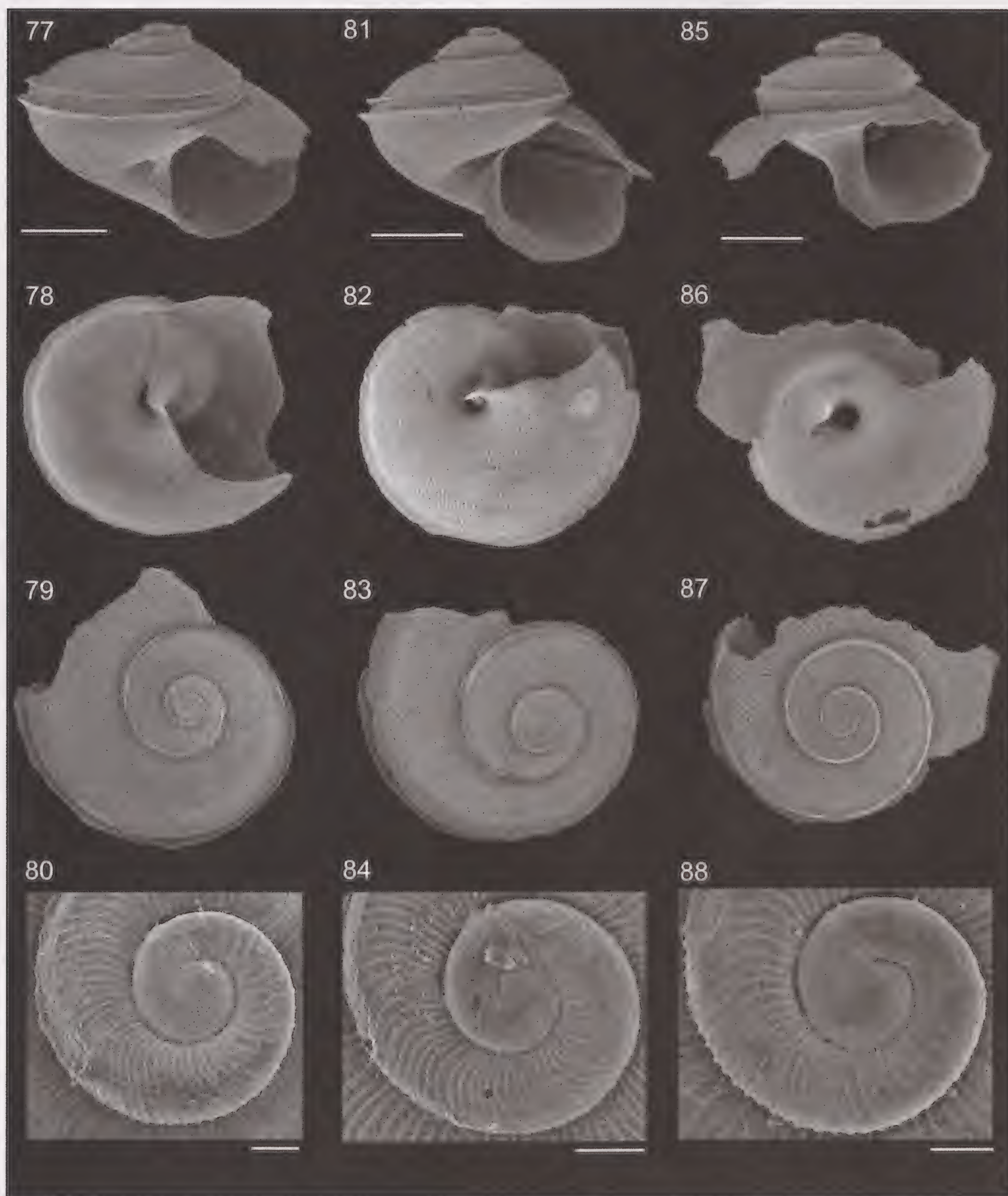
#### Description

Shell lenticular-discoid, spire depressed, up to 3.2 mm tall, 2.6 mm wide. Protoconch of ~ 0.8 whorl, with dense flocculent sculpture; faint apertural varix not connected to embryonic cap, somewhat convex apertural margin. Teleoconch I of ~ 0.75 whorl, with ~ 30 axial cords



reaching suture; interstices approximately three times width of cord, becoming narrower towards end of teleoconch I; spiral cord in position of selenizone present in some shells. Teleoconch II up to two whorls, suture strongly impressed; shoulder profile slightly convex, with

~ 100 axial cords extending to suture on second whorl, proportionally increasing in strength with growth from thin to thick cords, extending onto keel of selenizone; interspaces about as wide as width of cord, sometimes becoming larger towards apertural margin; spiral lines a quarter



FIGS. 77–88. *Anatoma atlantica*. FIGS. 77–80: MNHN; FIGS. 81–84: MZSP 113463; FIGS. 85–88: MNHN. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.



as wide as axial cords, running over them, forming slight thickenings at intersections, first spiral cord at onset of teleoconch II, ~ 15 on second whorl, increasing in number to ~ 20 at apertural margin. Sutsel low, from half as wide to as wide as selenizone. Base with constriction below selenizone, profile slightly rounded; ~ 130 axial cords as strong as on shoulder, regularly spaced, reaching edge of keel of selenizone; ~ 25 spiral cords, half as strong to as strong as axial ribs, interspaces as wide as width of ribs, not reaching keels of selenizone, running over axial ribs, forming slight thickenings at intersections. Umbilicus moderately narrow; funiculus indistinct. Aperture rounded, adumbilical portion slightly flared. Selenizone at periphery, moderately wide; lunules moderately strong, somewhat aligned to axial ribs; keels of moderate strength and elevation.

Radula. Described in Geiger (2012: 1028, fig. 838), but identified as *A. proxima*.

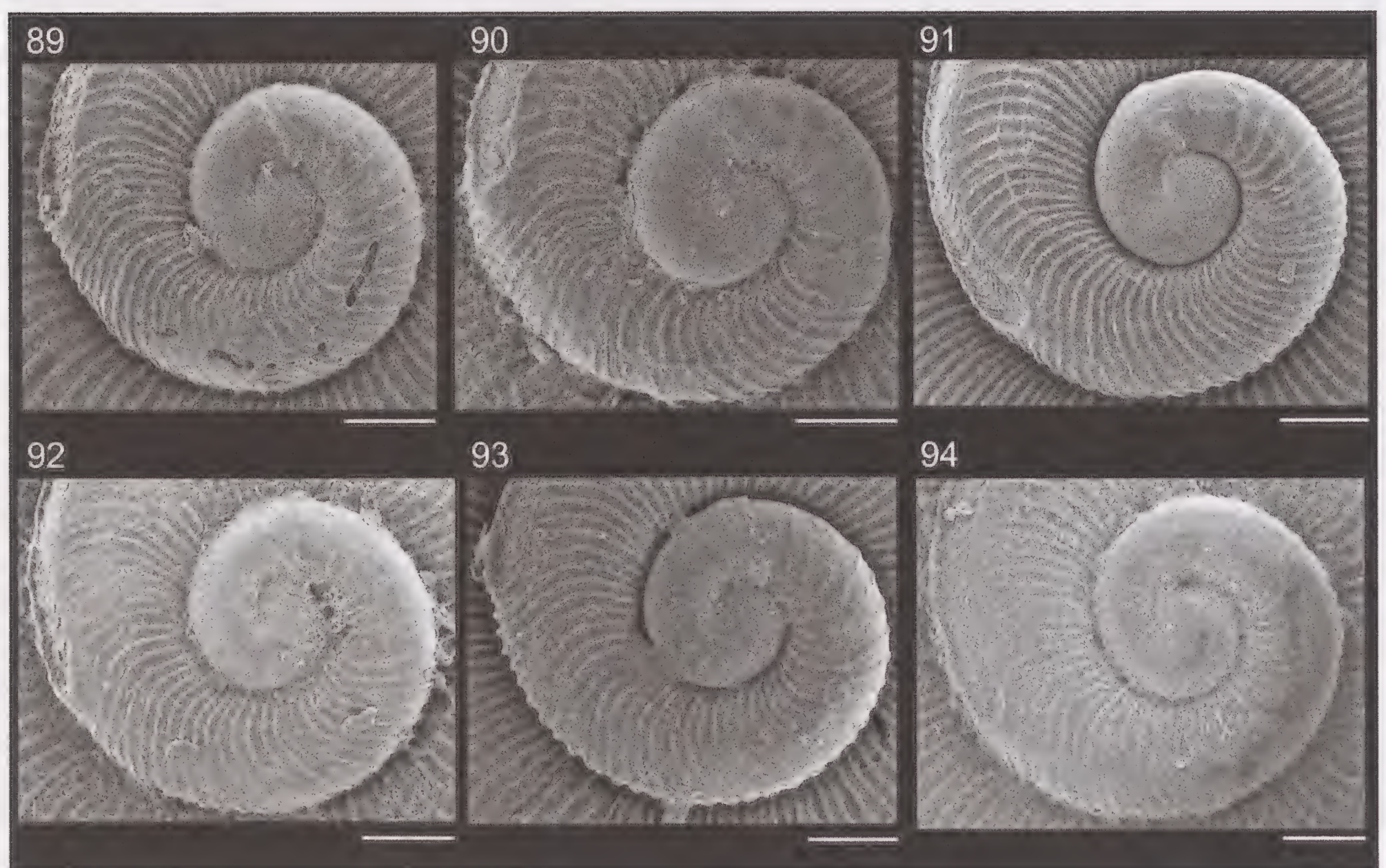
#### Remarks

*Anatoma atlantica* was described based on the holotype only, which, could not be located in collection of SGPIH (Ulrich Kotthoff, pers. comm.). Geiger (2012) considered *A. atlantica*

a valid species, but highlighted some “intriguing” aspects in the original description (Bandel, 1998), regarding its size and proportions. Anyway, Geiger (2012) presented a description and illustrated three shells from U.S.A. that are herein the basis for our interpretation of the morphological concept of *A. atlantica*, along with the original figure and description.

Geiger (2012) also highlighted the resemblance of *A. atlantica* with *A. proxima*, the main differences being the greater expansion rate of *A. atlantica*, its lenticular shape and less dense and pronounced sculpture. However, as stated above, under the remarks of *A. proxima*, we consider that some of the shells determined by Geiger (2012: fig. 836 A, B) as *A. proxima* are *A. atlantica*. Both shells in those figures have the lenticular shape and more dense sculpture. The change in delimiting the species is due to alternate weighting of characters (expansion rate vs. shell shape), and due to the additional material now available.

The additional material has also given further insights into shell characters. Bandel (1998) and Geiger (2012) described the teleoconch I of this species as lacking spiral sculpture based on material from the U.S.A. and the Caribbean. The spiral cord in the position of the seleni-



FIGS. 89–94. *Anatoma atlantica*. MNRJ 26613. Scale bars = 100  $\mu$ m.



zone on teleoconch I has now been frequently found to at least some degree in specimens from Brazil, while remaining the exception for northern specimens (e.g., FLMNH 249924). Figures 80, 84, 88 and 89–94 show the wide variation found in teleoconch I of the shells from Brazil. In some shells, a complete spiral cord, running from protoconch to onset of teleoconch I, is present (Fig. 80), sometimes it is eroded (Figs. 88, 90, 94), in other shells, the spiral cord is visible only close to protoconch, becoming less pronounced, tending to disappear close to onset of teleoconch II (Figs. 89, 94); in some cases, the axial ribs on teleoconch I have a slight thickening in the position of the disappeared/eroded spiral cord (Figs. 92, 93).

*Anatoma atlantica* from Brazil is strongly sculptured on the base of shell, with projecting axial ribs over the ventral edge of selenizone keel (Figs. 78, 82, 86) identical to the shells illustrated by Geiger (2012) and the protoconch sculpture is much more dense (Figs. 80, 88). Brazilian specimens tend to have coarser protoconch sculpture (Fig. 80) compared to the holotype and some northern specimens (Geiger, 2012: fig. 836A, B: fine; fig. 634B, C: coarse). Most of the Brazilian specimens have partially to fully eroded protoconchs (Figs. 93, 94).

*Anatoma atlantica* was described from Florida and recorded by Geiger (2012) from other localities in the Caribbean and south of U.S.A. In Brazil, it was collected in the northeast and southeastern coast.

#### Distribution

U.S.A.: South Carolina, Florida, Louisiana, Georgia; Mexico: Cozumel; Barbados; Brazil: Amapá, Pernambuco, Abrolhos Archipelago, Rio de Janeiro; 142 m to 1050 m.

#### *Anatoma copiosa*, n. sp. (Figs. 95–110)

*Anatoma aedonia* auctt., non Watson, 1886: Absalão (1989: 2, *partim*); Absalão et al. (2006: 229, in part.) [list of taxa].

*Anatoma proxima* auctt., non Dall, 1927: Geiger (2012, *partim*: fig. 837C).

#### Etymology

*Copiosus*, L. = abundant. Indicating that this is one of the most abundant *Anatoma* species in Brazil; also an allusion to its numerous spiral and axial cords.

#### Type Material

Holotype: MNRJ 16411.

Paratypes: *type locality*: MNRJ 17432, [1]; *Campos Basin, southeast Brazil*: HAB 16 sta. B–04 (23°10'0.72"S, 41°3'12.5"W, 107 m), 02/vii/2009: MNRJ 16444, [8]; HAB 11 sta. B–05 (23°11'25.8"S, 41°0'54.0"W, 150 m), 21/ii/2009: MNRJ 16436, [10]; HAB 11 sta. A–05 (23°36'10.3"S, 41°21'36.1"W, 142 m), 01/iii/2009: MNRJ 16418, [4]; MNHN IM–2012–2790, [4]; HAB 11 sta. G–04, Bazil (22°04'10.0"S, 40°7'5.80"W, 92 m), 25/ii/2009: MNRJ 16415, [4]; (22°42'S, 40°40'W, ~ 110 m), 19/ix/2003: MNRJ 16409, [6]; HAB 16 sta. B–04, (23°10'0.72"S, 41°3'12.5"W, 107 m), 02/vii/2009: SBMNH 230144, [5]; HAB13 sta. H–04, (21°42'49.3"S, 40°10'21.4"W, 98 m), 09/iii/2009: MZSP 118420, [4]; MNRJ 18167, [7]; 2003, P.M.S. Costa leg.: MORG 48552, [8]; *off Espírito Santo state*: 16/viii/1984, Oceanographic Ship *Almirante Saldanha* col.: IBUFRJ 19438, [6].

#### Type Locality

Campos Basin, southeast Brazil: HAB 11 sta. G–05, (22°06'06.2"S, 40°03'12.6"W, 154 m).

#### Additional material

*Brazil: off Espírito Santo state*: REVIZEE Central sta. C5–25A (19°33'S, 38°45'W, 230 m), 28/vi/2001: IBUFRJ 14012, [1]; REVIZEE Central sta. C1–VV24 (20°00'S, 39°54'W, 45 m), 27/ii/1996: MORG 52492, [4]; *Campos Basin*: HAB 13 sta. I–04 (21°22'55.2"S, 40°15'31.5"W, 103 m), 06/iii/2009: MNRJ 16414, [2]; HAB13 sta. H–05 (21°42'33"S, 40°09'05.9"W, 147 m), 09/iii/2009: MNRJ 16410, [3]; HAB13 sta. H–03 (21°43'05.9"S, 40°11'36.9"W, 73 m), 09/iii/2009: MNRJ 18185, [1]; HAB 11 sta. G–03 (22°03'41.2"S, 40°10'5.38"W, 75 m), 25/ii/2009: MNRJ 16412, [1]; HAB16 sta. G–04 (22°03'34.2"S, 40°07'05.5"W, 89 m), 06/vii/2009: MNRJ 16447, [1]; HAB 16 sta. G–05 (22°06'6.1"S, 40°03'12.8"W, 149 m), 07/vii/2009: MNRJ 16448, [3]; MNRJ 16432, [1]; MNRJ 17433, [2]; HAB 17 sta. D–04 (22°23'17.7"S, 40°35'05.2"W, 110 m), 25/vii/2009: MNRJ 16446, [1]; HAB 11 sta. D–05 (22°31'02.8"S, 40°31'38.6"W, 139 m), 22/ii/2009: MNRJ 16416, [1]; *off Macaé, Rio de Janeiro State* (22.995°S, 40.927°W, 110–220 m): DLG 105, [2]; (22°42'S, 40°40', ~ 110 m), 2007: MNRJ 17274, [40]; MNRJ 17073, [24];



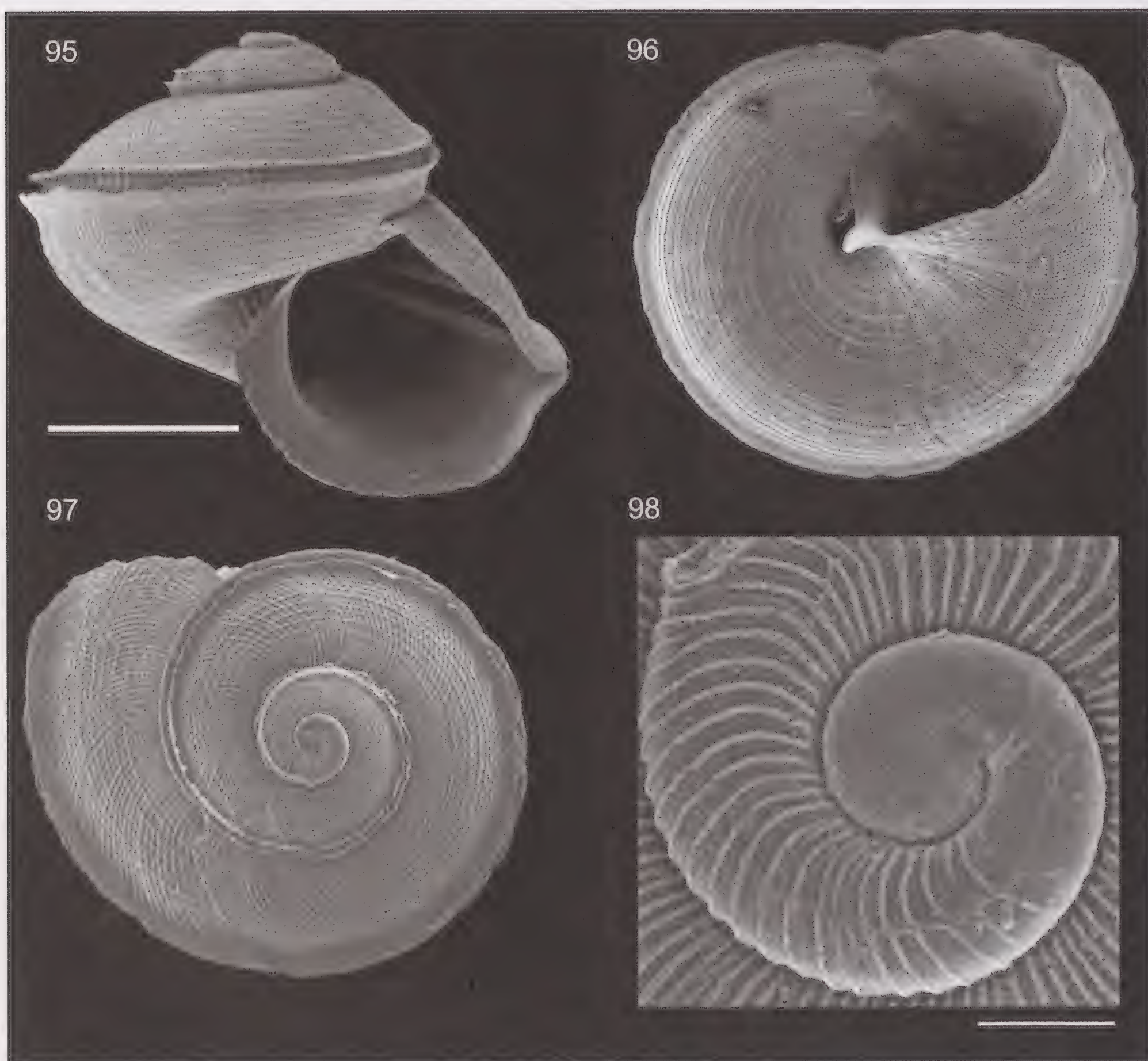
SBMNH 230143, [13]; MNRJ 30523, [7]; HAB 11 sta. C-03 (22°46'50.5"S, 41°03'39"W, 77 m), 22/ii/2009: MNRJ 16454, [1]; HAB 11 sta. C-04 (22°51'57.5"S, 40°57'35.1"W, 92 m), 22/ii/2009: MNRJ 16413, [3]; MNRJ 16445, [9]; REVIZEE Central sta. C1-D3 (22°52'S, 41°09'W, 80 m), 23/ii/1996: IBUFRJ 19437, [1]; HAB 11 sta. C-05 (22°57'23.9"S, 40°50'36.4"W, 142 m), 21/ii/2009: MNRJ 16417, [1]; (23°05'22.73"S, 40°58'55.52"W, ~ 100 m), 17/ix/2004: MORG 52520, [1]; HAB 11 sta. B-04 (23°10'0.2"S, 41°03'12.6"W, 107 m), 21/ii/2009: MNRJ 29799, [3]; HAB 16 sta. A-05 (23°36'10.4"S, 41°21'36.1"W, 145 m), 01/vii/2009: MNRJ 16443, [1]; (23°5.38'S, 40°58.45'W, 101 m), 18/x/2001: MNRJ 30521, [17]; iv/1998; sup-

ply boat *Astro Garoupa* col.: IBUFRJ 19441, [93]; 20-27/i/1998, supply boat *Astro Garoupa* col.: IBUFRJ 11786, [145]; IBUFRJ 11788, [1]; x/2008, P.M.S. Costa leg.: MNRJ 17262, [2]; 2003, P.M.S. Costa leg.: MORG 48587, [11]; MORG 48341, [7]; MORG 48178, [6]; MORG 48292, [9]; MORG 48134, [8].

Material of *Anatoma* cf. *copiosa*: Louisiana, U.S.A. (28.093°N, 91.011°W, 70.8 m): EGC 24459, [1].

#### Diagnosis

Trochiform shell with very low sutsel, very dense axial and spiral sculpture on shoulder; base with very faint axial lines.



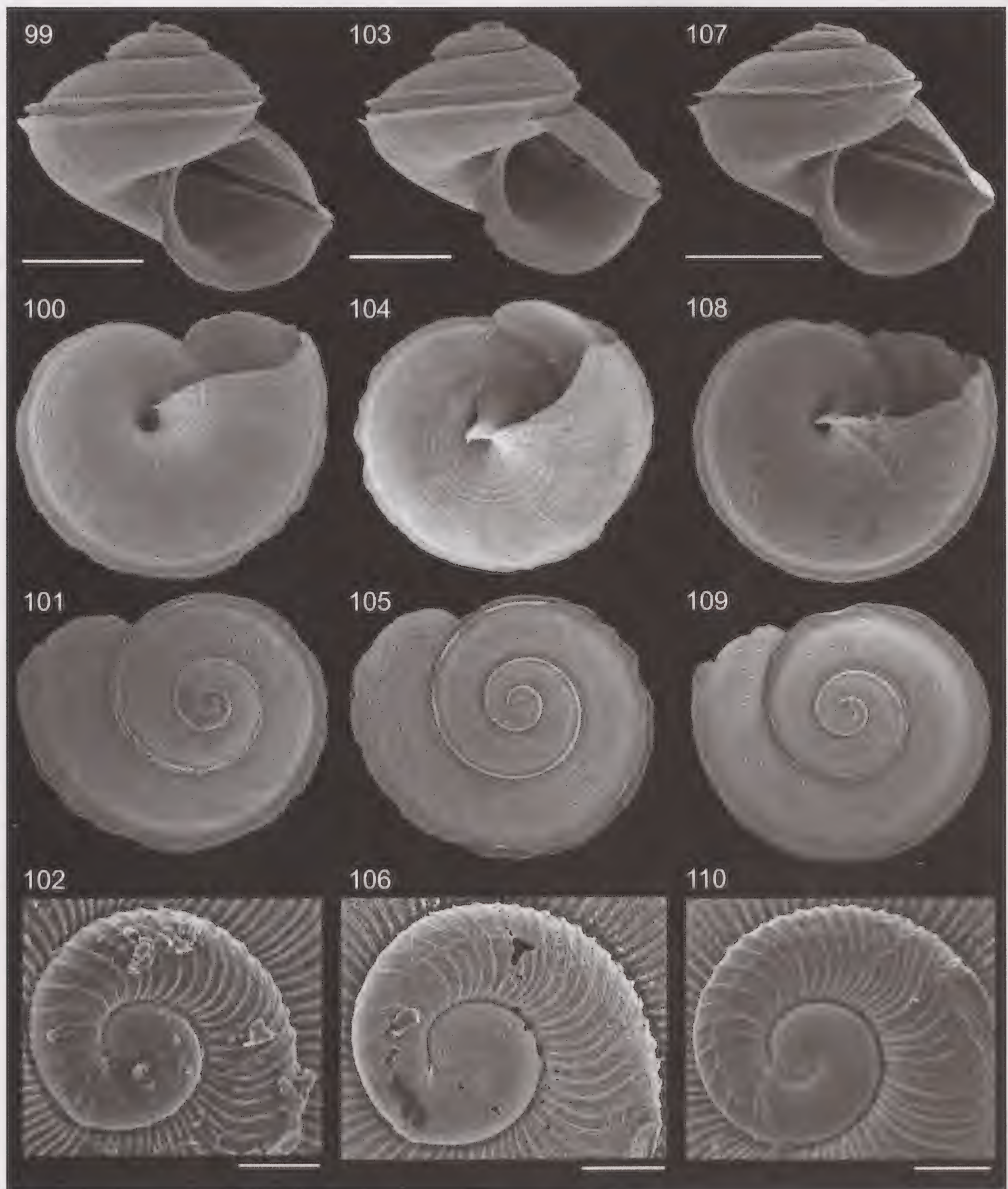
FIGS. 95–98. *Anatoma copiosa*, n. sp., Holotype. Scale bars: whole shells = 1 mm, details = 100 µm.



## Description

Shell trochiform, lenticular-discoïd, spire depressed, slightly wider than tall, 2.5 mm tall, 2.8 mm wide (holotype). Protoconch of ~ 0.8 whorl, with very fine flocculent sculpture;

apertural varix indistinct, not connected to embryonic cap, apertural margin straight to shallow sinusoid. Teleoconch I of ~ 0.75 whorl, with ~ 25 axial cords most reaching suture; interstices approximately three times width of cords, low density irregular flocculations;



FIGS. 99–110. *Anatoma copiosa*, n. sp., Paratypes. FIGS. 99–102: MNRJ 16436; FIGS. 103–106: MNRJ 16409; FIGS. 107–110: MNRJ 16415. Scale bars: whole shells = 1 mm, details = 100 µm.



spiral cord in position of selenizone, tending to disappear towards end of teleoconch I. Teleoconch II up to 2.5 whorls, suture strongly impressed; shoulder slightly convex, with ~ 120 axial cords reaching suture on second whorl, proportionally increasing in strength with growth from thin to thick cords, not reaching edge of keel of selenizone; interspaces about as wide as width of cords; spiral cords usually stronger than axial cords, much weaker adjacent to suture, running over them, forming slight thickenings at intersections, first spiral cord at onset of teleoconch II, ~ 8 on second whorl, ~ 15 at apertural margin. Sutsel very low, approximately half width of selenizone after one teleoconch II whorl. Base with faint constriction below selenizone, profile slightly rounded; axials very faint, almost growth lines, slightly stronger at apertural margin, not reaching keel of selenizone; about 15 spiral cords, stronger than axials, irregularly spaced. Umbilicus of moderately width, funiculus distinct. Aperture rounded, adumbilical portion slightly flared. Selenizone at periphery, moderately wide; lunules moderately strong, regularly spaced, not aligned to axials; keels of moderate strength and elevation. Animal unknown.

#### Remarks

*Anatoma copiosa* n. sp. (Figs. 95–110) is the most abundant species in southeaster Brazil. All shells examined have a characteristic spiral cord on teleoconch I, usually fading before the onset of the selenizone (Figs. 98, 102, 106, 110), and faint sculpture on the base, where the spiral cords are very slender and irregularly spaced, with some wider interspaces in the middle of the whorl, and the axials are almost as weak as growth lines (Figs. 96, 100, 104, 108). *Anatoma copiosa* is very similar to *A. atlantica* (Figs. 77–88) with respect to the trochiform shell shape, shoulder sculpture, and teleoconch I. *Anatoma atlantica* has much stronger sculpture on the base and strong markings on the keels of the selenizone. It differs from *A. proxima* by the presence of a spiral cord in position of the selenizone on early teleoconch I whorl and the finer axial sculpture and the more irregularly spaced spiral cords on the base.

Among the species from Brazil, *A. copiosa* and *A. alternatisculpta* are extremely abundant in the samples from southeast Brazil, being collected together in many stations from Campos Basin. Both species have very similar shell

shapes with low sutsel, but the sculpture of *A. copiosa* (Figs. 95–97, 98–100, 102–104, 106–108) is much more dense than that of *A. alternatisculpta* (Figs. 111–131).

A single shell from off Louisiana, U.S.A. (70.8 m) is very similar in shape and sculpture, but lacks the spiral cord in teleoconch I. Given such minor difference and the discrepancy in occurrence, we consider it as an unresolved record.

#### Distribution

Brazil: Espírito Santo and Rio de Janeiro; 45 m to 230 m.

*Anatoma alternatisculpta*  
Geiger & McLean, 2010  
(Figs. 111–131)

*Anatoma alternatisculpta* Geiger & McLean, 2010: 15, figs. 11, 12; Geiger (2012: 756, figs. 608–610).

*Anatoma aedonia* auctt., non Watson, 1886: Absalão (1989: 2, *partim*) [list of taxa]; Absalão et al. (2006: 229, *partim*) [list of taxa]. *Anatoma* sp.: Leal (1991: 43, pl. 2, figs. L–M); Absalão et al. (2006: 229, *partim*) [list of taxa].

#### Type Material

Holotype: USNM 1132066.

Paratypes: USNM 1132067, type locality [9]; USNM 500678, 137–146 m, off Pelican Island, Barbados (13.167°N, 59.567°W) [15]; USNM 1132065, 165–183 m, off Lazaretto, Barbados (13.133°N, 59.617°W) [1].

#### Type Locality

137 m, off Pelican Island, Barbados, 13.167°N, 59.567°W.

#### Material Examined

U.S.A.: Florida: off Fernandina (30.669°N, 81.463°W 538 m): USNM ex 108147 [5].

Barbados: off Pelican Island (13.166°N, 59.567°W, 268 m): USNM ex 500677, [4]; off Pelican Island (13.167°N, 59.567°W, 60 m): USNM 1233934 (USNM ex 500679): [1].

Brazil: off Amapá state: (04°27'54"N, 49°58'05"W, 160 m), 13/x/2000, P. M. S. Costa leg.: MNRJ 26753, [1]; off Bahia State: REVIZEE Central sta. C1–C76 (15°53'49"S,



38°31'57"W, 65 m), 30/iv/1996: IBUFRJ 10120, [1]; REVIZEE Central sta. C2–16 (18°03'S, 37°18'W, 82 m), 23/xi/1997: IBUFRJ 13976, [1]; IBUFRJ 14537, [1]; *off Espírito Santo State*: Oceanographic Ship *Almirante Saldanha* col., 16/viii/1984: IBUFRJ 19439, [4]; REVIZEE Central sta. C2–17 (18°34'S, 38°04'W, 55 m), 22/xi/1997: IBUFRJ 14059, [5]; REVIZEE Central sta. C5–20R (19°16'S, 38°00'W, 67 m), 28/vi/2001: IBUFRJ 13799, [1]; REVIZEE Central sta. C1–C64 (19°17'42"S, 38°42'02"W, 63 m), 25/iv/1996: IBUFRJ 9257, [2]; IBUFRJ 12774, [5]; REVIZEE Central sta. C1–VV38 (19°28'S, 38°22'W, 71.4 m), 29/ii/1996: IBUFRJ 9834, [+800]; REVIZEE Central sta. C1–VV24 (20°00'S, 39°54'W, 45 m), 27/ii/1996: MORG 40560, [4]; *off Vitória*, 50 m, Oc. Ship *Victor Hansen* coll., iii/1994: MORG 39430, [2]; REVIZEE Central sta. C1–VV22 (20°20'S, 40°05'W, 33 m), 27/ii/1996: MORG 41520, [1]; REVIZEE Central sta. C1–VV21 (20°38'S, 40°00'W, 56 m), 27/ii/1996: IBUFRJ 12770, [1]; MORG 41093, [1]; *Vitória Seamount, Vitória-Trindade Chain*: REVIZEE Central sta. C1–C62 (20°30'02"S, 39°28'51"W, 96 m), 25/iv/1996: IBUFRJ 9535, [5, complete]; MNRJ 15675, [2]; REVIZEE Central sta. C1–C61 (20°30'38"S, 37°19'06"W, 88 m), 24/iv/1996: IBUFRJ 10193, [12]; *Jasseur Seamount, Vitória-Trindade Chain*: MD 55 sta. 21–DC35 (20°42'S, 35°22'W, 82–105 m): MNRJ 17003, [1]; *Campos Basin*: HAB13 sta. I–02 (21°22'54.6"S, 40°19'48.4"W, 52 m), 05/iii/2009: MNRJ 29795, [1]; HAB13 sta. I–04 (21°22'55.2"S, 40°15'31.5"W, 103 m), 06/iii/2009: MNRJ 16431, [1]; HAB13 sta. H–04 (21°42'49.3"S, 40°10'21.4"W, 98 m), 09/iii/2009: MNRJ 16424, [12]; SBMNH 230146, [8]; MNRJ 16408, [1]; HAB13 sta. H–05 (21°42'33"S, 40°09'05.9"W, 147 m), 09/iii/2009: MNRJ 16428, [4]; HAB13 sta. H–03 (21°43'05.9"S, 40°11'36.9"W, 73 m), 09/iii/2009: MNRJ 16429, [6]; HAB16 sta. G–04 (22°03'34.2"S, 40°07'05.5"W, 89 m), 06/vii/2009: MNRJ 16451, [1]; HAB11 sta. G–03 (22°03'41.2"S, 40°10'5.38"W, 75 m), 25/ii/2009: MNRJ 16421, [5]; HAB11 sta. G–04 (22°04'10.0"S, 40°7'5.80"W, 92 m), 25/ii/2009: MNRJ 16423, [9]; HAB11 sta. D–05 (22°31'02.8"S, 40°31'38.6"W, 139 m), 22/ii/2009: MNRJ 16430, [1]; *Campos Basin* (22°42'S, 40°40', ~ 110 m), 2007: MNRJ 30524, [1]; (22°42'S, 40°40', ~ 110 m), 19/ix/2003: MNRJ 16419 [3]; HAB11 sta. C–03 (22°46'50.5"S, 41°03'39"W, 77 m), 22/ii/2009: MNRJ 29786, [1, complete]; HAB 11 sta. C–04 (22°51'57.5"S, 40°57'35.1"W, 92 m), 22/ii/2009:

MNRJ 16450, [9]; MNRJ 16452, [2]; MNRJ 16426, [5]; (23°05'22.73"S, 40°58'55.52", ~ 100 m): MNRJ 16420 [5]; MNRJ 17231 [4]; MNRJ 30522 [8]; (23°05'22.73"S, 40°58'55.52", ~ 100 m), 17/ix/2004: MORG 50118, [3]; HAB11 sta. B–04 (23°10'0.72"S, 41°3'12.5"W, 107 m), 02/vii/2009: MNRJ 16434, [1]; MNRJ 16425, [1]; HAB 16 sta. B–04 (23°10'0.72"S, 41°3'12.5"W, 107 m), 02/vii/2009: MNRJ 16449, [18]; SBMNH 230147, [9]; HAB11 sta. B–05 (23°11'25.8"S, 41°0'54.0"W, 150 m), 21/ii/2009: MNRJ 16437, [13]; HAB11 sta. A–05 (23°36'10.3"S, 41°21'36.1"W, 142 m), 01/iii/2009: MNRJ 16422, [2]; (23°05'22.73"S, 40°58'55.52", ~ 100 m): MNRJ 17275, [1]; MNRJ 17072 [2]; iv/1998, supply boat *Astro Garoupa* coll.: IBUFRJ 11787, [28]; 20–27/i/1998, supply boat *Astro Garoupa* coll. IBUFRJ 19440, [29]; 2003, P.M.S. Costa leg.: MORG 48103, [11]; MORG 48263, [11]; MORG 48515, [10]; *São Paulo state*: (24°40'S, 44°52'W, 134 m), 08/v/1970: MZSP 35064 [25]; MZSP 113474 [15]; MZSP 113461 [2]; MZSP 113472 [1]; MZSP 113471 [1]; MZSP 113468 [1]; MZSP 113466 [23]; *Rio Grande do Sul State*: *off Chuí* (166 m) Research Vessel *W. Besnard* coll., 17/i/1972: MORG 17312, [1].

#### Description

See Geiger (2012).

#### Remarks

The material of *A. alternatisculpta* from Brazil here examined agrees with the original description with respect to the shell shape with low sutsel, protoconch with scarce flocculent sculpture and general sculpture pattern on teleoconch I and II.

Some variability in several characters is present in this taxon. The holotype (Geiger, 2012: fig. 608) has a more elevated spire with a wide sutsel, while most shells from Brazil and some paratypes have a more narrow sutsel (Figs. 111, 115, 119). The holotype with 2.75 whorls is also larger than the paratypes and the material from Brazil. The ontogenetic trend of taller shell and wider sutsel is well-known in many *Anatoma* species (Geiger, 2012).

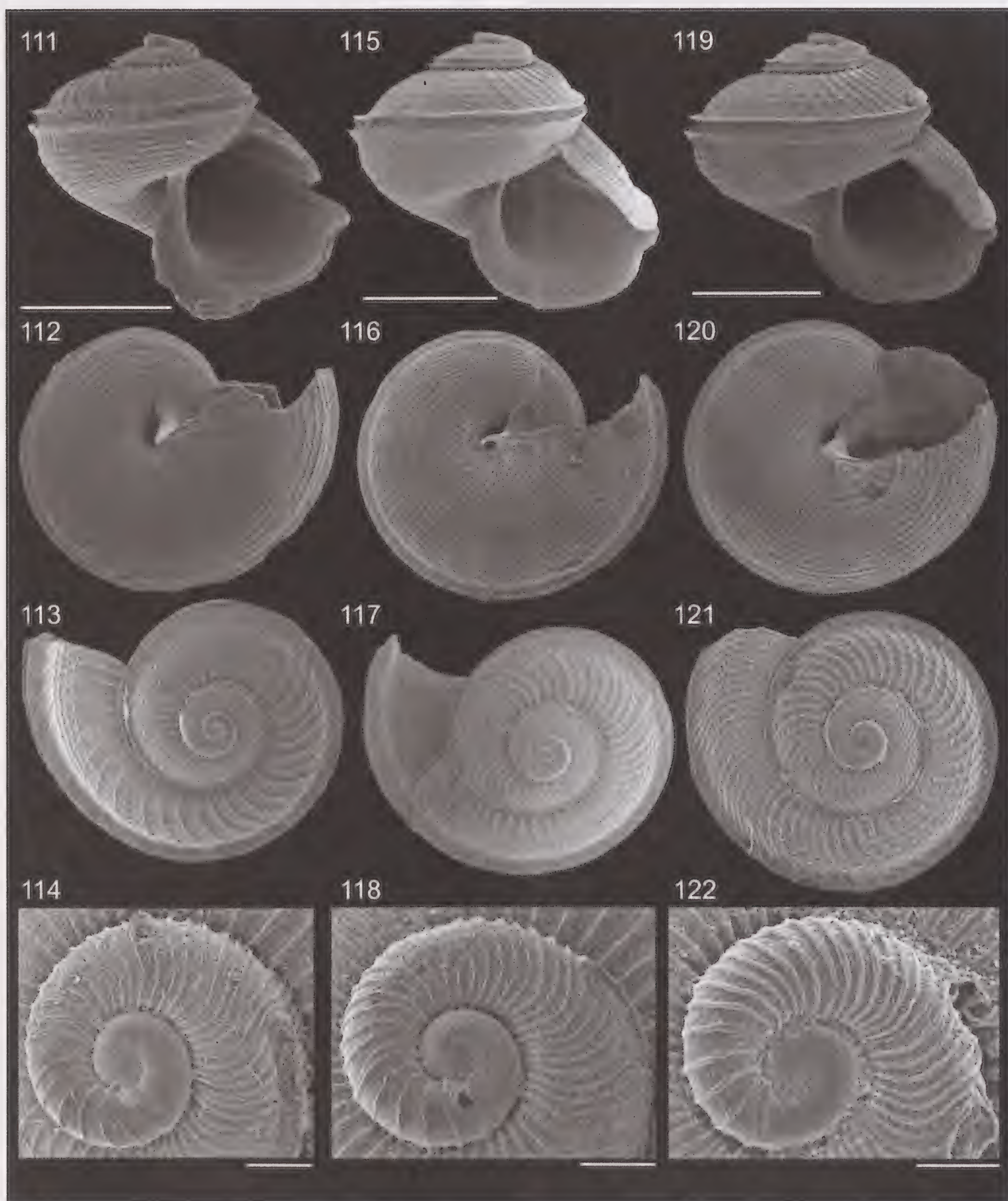
The original description mentioned that teleoconch I has 14–19 axial ribs, and some shells have a spiral cord on position of selenizone. In the shells from Brazil, the number of axial ribs reaches 25, and a spiral cord is almost never present (Figs. 114, 118, 122); a vestigial cord can be seen in some shells (Fig. 125).



Geiger & McLean (2010) described *A. alternatisculpta* based on ten specimens with 3–4 thick spiral cords at the apertural margin, concentrated in the middle of shoulder. The much more numerous Brazilian material documents a wider range: 4–10 (Figs. 126–131). The thick-

enings at the intersection between axials and spirals vary in distinctness (Figs. 126–131).

The peripheral termination of the axial cords ranges from the onset of the keel of selenizone to its edge (Fig. 127 vs. Fig. 130). All those variation can also be observed in the type series, il-



FIGS. 111–122. *Anatoma alternatisculpta*. FIGS. 111–114: MNRJ 16437; FIGS. 115–118: MNRJ 16423; FIGS. 119–122: MNRJ 17231. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.



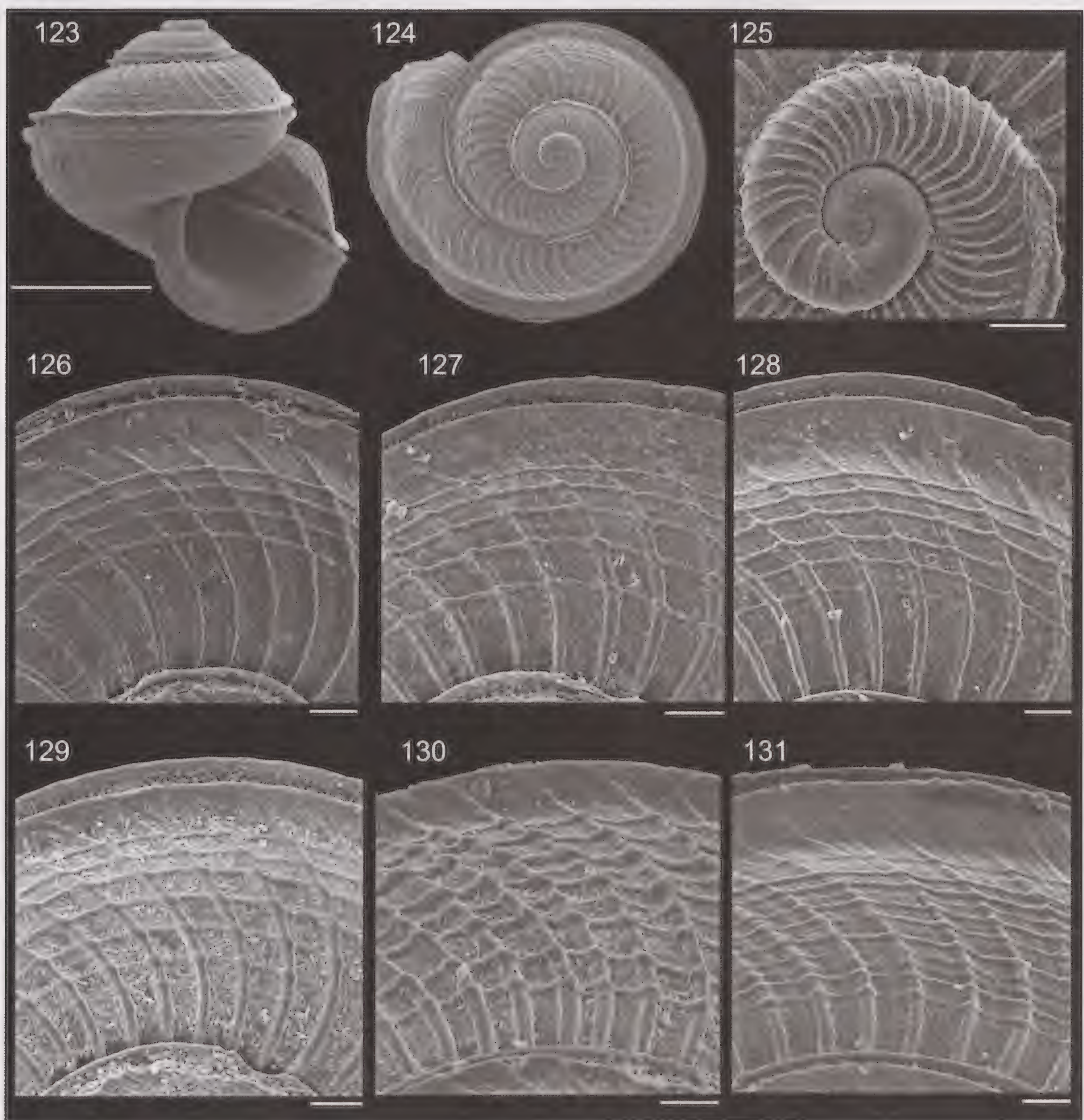
illustrated by Geiger (2012). We consider all those differences as minor intraspecific variation.

*Anatoma alternatisculpta* was described from Barbados and was up to now known only from the type locality (Geiger, 2012). However, in Brazil, this species is very abundant along the central coast, from south of Bahia state to the coast of São Paulo state, besides a single record from South Brazil. In addition, the figured shell in Leal (1991), determined as *Anatoma* sp. is, in fact, *A. alternatisculpta* from Jas-

sauer Bank, in the Vitoria-Trindade Chain, that matches the distribution here stated, including records from Vitória seamount in the same chain of submarine mounts.

#### Distribution

U.S.A.: Florida; Barbados; Brazil: Amapá, Bahia to São Paulo, Vitória and Jasseur seamounts, Rio Grande do Sul; 25 m to 183 m (a single shell from Florida in 538 m).



FIGS. 123–131. *Anatoma alternatisculpta*. FIGS. 123–125, 131: MNRJ 16419; FIG. 126: MNRJ 16437; FIG. 127: MNRJ 16423; FIG. 128: MNRJ 16437; FIG. 129: MNRJ 17231; FIG. 130: MNRJ 17231. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.



***Anatoma espiritosantense*, n. sp.**  
(Figs. 132–147)

*Anatoma aedonia* auctt., non Watson, 1886:  
Absalão et al. (2006, *partim*: 229) [list of  
taxa].

*Anatoma* sp.: Absalão et al. (2006, *partim*: 229)  
[list of taxa].

**Diagnosis**

Trochiform to globose shell with dense axial  
ribs irregularly distributed over shoulder, with  
randomly distributed wider interspaces.

**Etymology**

Espiritosantense is a locative, referring to  
the state of Espírito Santo, in Brazil. Also the  
Portuguese gentile for people born in Espírito  
Santo state, although very rarely used.

**Type Material**

Holotype: MNRJ 17000.

Paratypes: *type locality*: IBUFRJ 18755, [17];  
MNRJ 30527, [10]; SBMNH 230145, [3]; MNHN  
IM-2012-2791 [2]; *Vitória Seamount, Vitória-  
Trindade Chain*: REVIZEE Central sta. C1-61



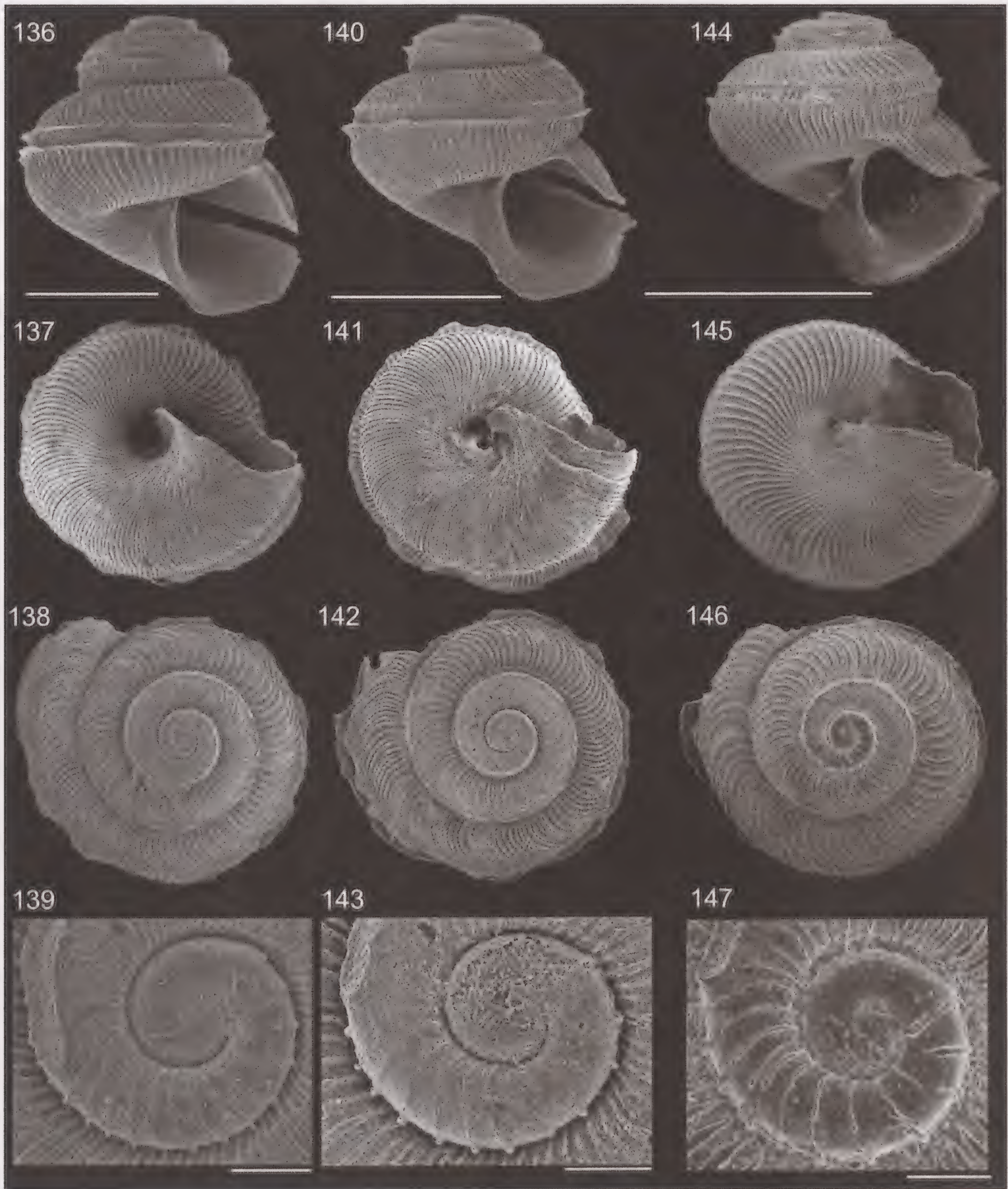
FIGS. 132–135. *Anatoma espiritosantense*, n. sp., Holotype. Scale bars: whole shells = 1 mm, details = 100 µm.



(20°30'38"S, 37°19'06"W, 88 m), 24/iv/1996: IBUFRJ 9393, [1]; IBUFRJ 10192, [3]; *continental shelf of Campos Basin, Rio de Janeiro state*: HAB13 sta. H-04 (21°42'49.3"S, 40°10'21.4"W, 98 m), 09/iii/2009: MNRJ 30528, [1].

## Type Locality

Continental shelf of Espírito Santo state, Brazil: REVIZEE Central sta. C1-VV38 (19°28'S, 38°22'W, 71 m).



FIGS. 136–147. *Anatoma espiritosantense*, n. sp., Paratypes. FIGS. 136–143: MNRJ 30527; FIGS. 144–147: SBNHM 230145. Scale bars: whole shells = 1 mm, details = 100 µm.



## Description

Shell trochiform to globose, almost as tall as wide, spire turreted, 1.7 mm tall, 1.5 mm wide (holotype). Protoconch of ~ 0.8 whorl, sculpture much eroded in almost all shells, with some irregular granules still visible in some regions, apertural varix not connected to embryonic cap, apertural margin straight. Teleoconch I of ~ 0.6 whorl, ~ 12 axial cords, most extending from upper to lower suture; interstices approximately three times width of cords, covered by microscopic irregular concretions or smooth; no spirals. Teleoconch II up to three whorls, suture strongly impressed; shoulder profile strongly convex, with ~ 65 axial ribs reaching suture on second whorl, denser on first whorl, then more irregularly spaced, becoming denser close to apertural margin, proportionally increasing in strength with growth from thin cords to thick, forwardly-inclined ribs, reaching edge of keel of selenizone; interspaces usually about half width of ribs, very irregularly spaced over shoulder, with random wider interspaces; spiral lines running over axial ribs, forming slightly thickening at intersections, first spiral cord after 0.5 teleoconch II whorl, ~ 10 on second whorl, 18 at apertural margin. Sutsel twice as wide as selenizone at first teleoconch II whorl. Base with distinct constriction below selenizone, profile rounded; sculpture of similar density and strength as on shoulder, reaching keels of selenizone; ~ 25 indistinct spiral lines. Umbilicus of moderately width, funiculus distinct. Aperture rounded, adumbilical portion slightly flared. Selenizone at periphery, moderately wide; lunules numerous, approximately twice as dense as axial ribs, moderately strong, regularly spaced; keels short, of moderate strength and elevation, usually broken. Animal unknown.

## Remarks

*Anatoma espiritosantense* n. sp. (Figs. 132–147) is clearly distinguished from all other species from Brazil by its globose shell with a high spire and strongly convex profile of the shoulder. The other species herein described with turreted spire, *A. aedonia* and *A. proxima*, have a trochiform general shape, not globose.

The sculpture of *A. espiritosantense* is unique among the species from Brazil. The strong axial ribs, with irregular spacing (Figs. 134, 138, 142, 146) set it apart immediately.

Globally, the most similar species is *Anatoma quadraxialis* Geiger, 2012, from the Indo-Malayan Archipelago. It shares the overall shell shape and the dense, forward-slanted axial ribs. It can be distinguished by the reticulate protoconch sculpture and additional axial lines between the axial lamellae on the keels of the selenizone. *Anatoma rolani* Geiger & Fernández-Garcés, 2010, from the Caribbean shares the dense, forward-slanted axial ribs, but has a smooth protoconch without apertural varix, and has an overall lenticular shell shape with a narrower umbilicus. *Anatoma aspera* (Philippi, 1844) from West Africa, Europe and the Mediterranean, has a similar globose shell shape and sculpture pattern, but lacks the irregular axial rib spacing on shoulder, and teleoconch I has a strong spiral cord. All the above species were discussed and figured by Geiger (2012).

## Distribution

Brazil: Espírito Santo and Rio de Janeiro, Vitória seamount. 71 m to 98 m.

***Anatoma campense*, n. sp.**  
(Figs. 148–155)

*Anatoma* sp.: Absalão et al. (2006, *partim*: 229) [list of taxa].

## Diagnosis

Biconical shell, with strongly projected apertural margin and keel of selenizone; teleoconch I with approximately one whorl with a strong spiral cord; sculpture of base extending over abapical keels of selenizone.

## Type Material

Holotype: MNRJ 17002.

Paratypes: *Campos Basin*: Oceanprof I, sta. 44 (22°10'43"S, 39°54'46"W, 750 m), 10/xii/2002: IBUFRJ 19756, [1]; MNRJ 26703, [2]; Oceanprof II, sta. 44 (22°10'43"S, 39°54'46"W, 750 m), 01/vii/2003: IBUFRJ 19656, [1]; Oceanprof I sta. 74 (22°27'31"S, 40°09'23"W, 750 m), 21/xi/2002: IBUFRJ 15416, [1]; Oceanprof II sta. 74 (22°27'31"S, 40°09'23"W, 749 m), 18/vi/2003: IBUFRJ 17281, [2]; MNHN IM-2012-2792, [1]; *Paraná state*: off Paranaguá (26°15.14'S, 46°54.35'W, 686 m), NOWB coll., 26/v/2001: MZSP 36786, [1, complete].



## Type Locality

Continental slope of Campos Basin, Rio de Janeiro state, southeastern Brazil; Oceanprof I sta. 59 (21°52'59"S, 39°55'30"W, 750 m).

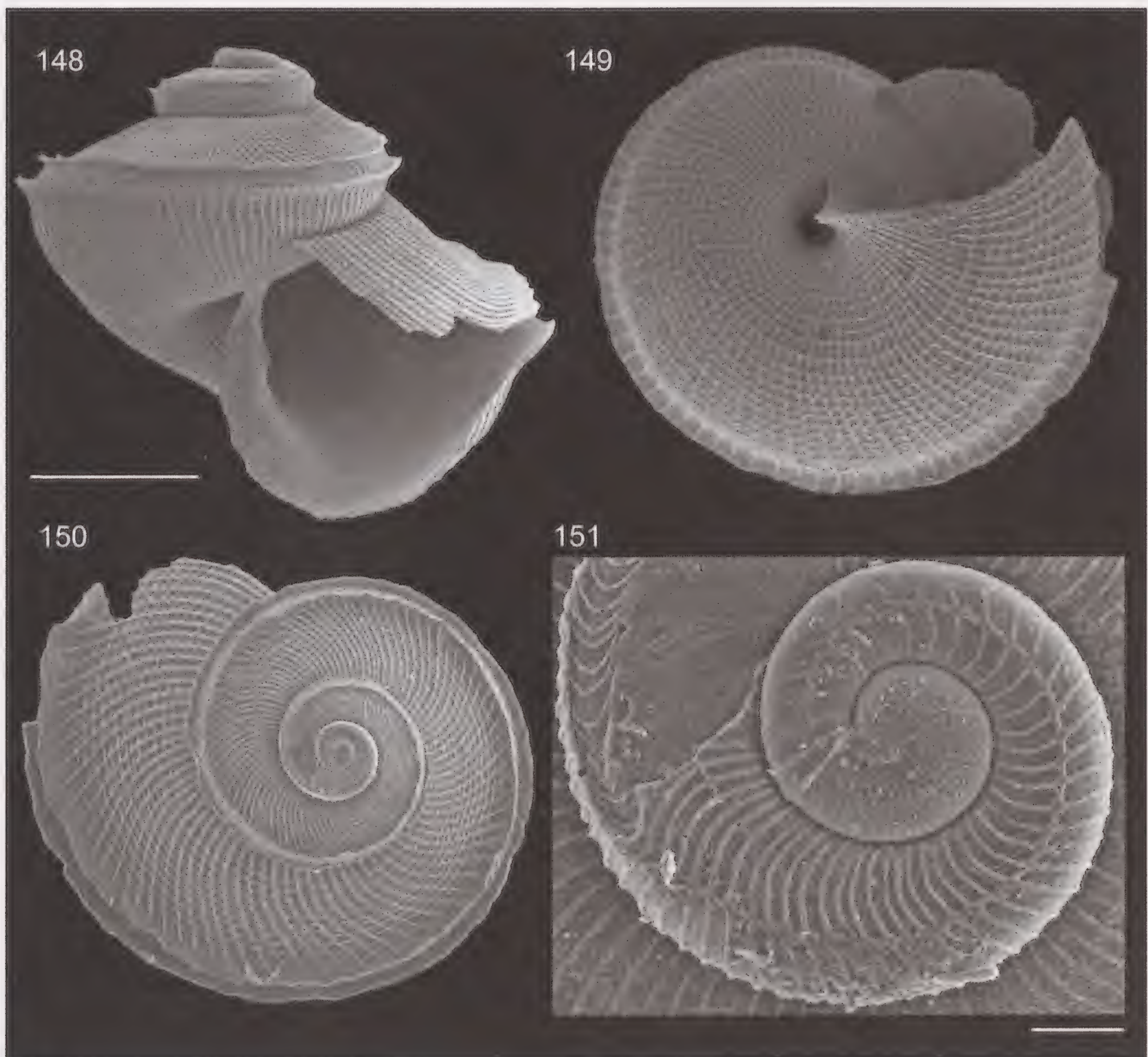
## Etymology

Campense is a locative, referring to the city of Campos, in Brazil. Also the Portuguese gentile for people born in Campos city.

## Description

Shell biconical, spire turreted, slightly wider than tall, 2.8 mm high, 3.1 mm wide (holotype).

Protoconch of ~ 0.8 whorl, sculpture flocculent, weak apertural varix not connected to embryonic cap; apertural margin straight. Teleoconch I of ~ 1 whorl, ~ 40 axial cords reaching upper suture becoming denser towards onset of selenizone; interstices smooth, ~ 3x as wide as cords at onset of teleoconch I, becoming narrower (~ 2x width of cord) towards onset of selenizone; well-developed spiral cord in position of selenizone, forming small nodules when crossing axial ribs. Teleoconch II of up to 2.5 whorls, suture strongly impressed; shoulder profile straight, with ~ 80 axial ribs on second whorl, partially extending onto keel of selenizone, proportionally increasing in strength with growth from thin to thick cords, interspaces about as wide as cords at



FIGS. 148–151. *Anatoma campense*, n. sp., Holotype. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.

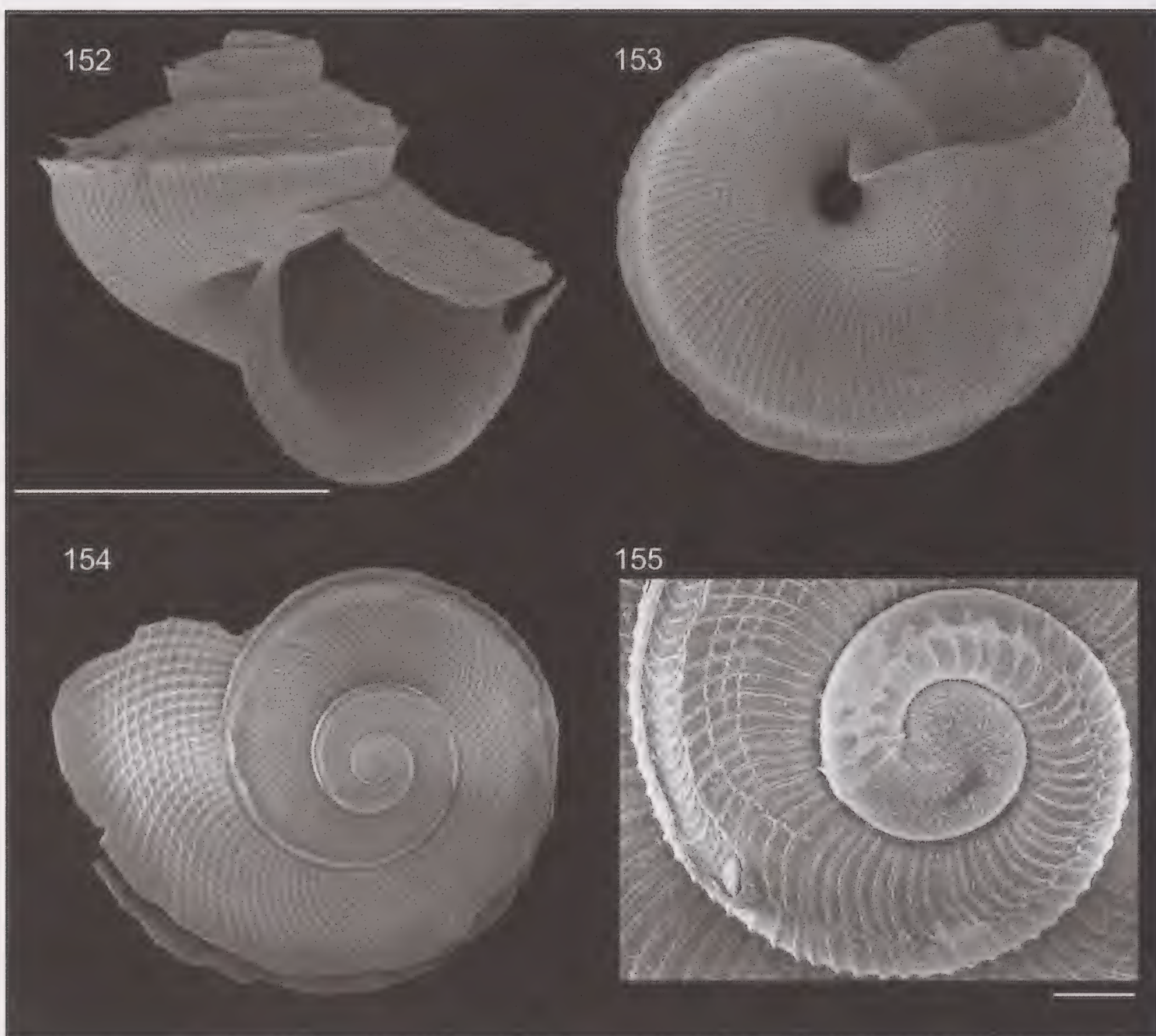


suture, twice as wide near selenizone; spiral lines about half as strong as axial ribs, running over them, forming slightly elevated thickenings, first spiral line at onset of selenizone, ~ 10 on second whorl, 12–15 at apertural margin. Sutsel ~ 2x selenizone width at first whorl of teleoconch II. Base with weak constriction below selenizone, profile slightly rounded; axial ribs of same strength and density as on shoulder, reaching edge of keel of selenizone; ~ 30 spiral cords, almost as strong as axial ribs, running over them, forming slightly thickening at intersections, extending onto keel of selenizone. Umbilicus of moderate width, no funiculus. Aperture rounded, adumbilical portion strongly flared. Selenizone at periphery, moderately wide; keels of moderate strength and elevation, somewhat adapically

deflected; lunules distinct, more or less aligned to axial ribs on base. Animal unknown.

#### Remarks

*Anatoma campense* (Figs. 148–155) is the largest *Anatoma* species from Brazil, with a well-projecting aperture. It shares with *A. aedonia* (Figs. 1–16) the long teleoconch I with approximately one whorl, bearing a strong spiral cord; the spire is also somewhat similar, but in *A. campense*, the well-projecting base and apertural margin give the shell a biconical general shape (Figs. 148, 152). The axial and spiral sculpture in *A. campense* is much denser both on shoulder and base (Figs. 148, 149, 152, 153).



FIGS. 152–155. *Anatoma campense*, n. sp., Paratype. MNRJ 26703. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.



*Anatoma campense* shares with *A. atlantica* (Figs. 77–94) the strongly, adapically deflected keel of the selenizone (Figs. 148, 152) and that the sculpture on the base is strong and extending onto the keel of the selenizone (Figs. 149, 153). However, in *A. atlantica* the spire is depressed with a very low sutsel.

*Anatoma amydra* Geiger & Marshall, 2012, from the Indo-Malayan Archipelago and *Anatoma biconica* Geiger, 2012, from the Indian Ocean to the Central Pacific are similar species, both have a turreted spire and similar sculpture on the base. However, *A. amydra* has a shorter teleoconch I (0.75 vs. 1 whorl) and denser sculpture on shoulder and base with interspaces only as wide as axial cords, not at least twice as wide. *Anatoma biconica* has

a more rounded profile of shoulder and base, and the spiral lines are much finer compared to the axial cords.

#### Distribution

Brazil: Rio de Janeiro, Paraná; 686 m to 750 m.

#### *Anatoma brychia*, n. sp. (Figs. 156–163)

#### Diagnosis

Large discoidal shell, with very thin sculpture on first teleoconch II whorl; teleoconch I large, ~ 1.25 whorls, with very thin spiral cord in position of selenizone; umbilicus wide.



FIGS. 156–159. *Anatoma brychia*, n. sp., Holotype. Scale bars: whole shells: 1 mm, details = 100 µm.



## Type Material

Holotype: MNRJ 26732.

Paratypes (all from Campos Basin, off Rio de Janeiro state, Brazil): Oceanprof II sta. 63 (21°52'43"S, 39°40'41"W, 1,941 m), 26/vi/2003: IBUFRJ 19704, [1]; Oceanprof II sta. 48 (22°11'16"S, 39°43'44"W, 1,068 m), 22/vi/2003: MNRJ 26733, [1]; MNRJ 26734, [1]; Oceanprof II sta. 83 (22°30'34"S, 39°51'44"W, 1,970 m), 16/vi/2003: IBUFRJ 19703, [1].

## Additional Material

*Anatoma* cf. *brychia*: off Georgia, U.S.A. (30.700°N, 79.000°W, 805 m): USNM 108420, [6].

## Type Locality

Continental slope of Campos Basin, Rio de Janeiro state, Brazil; Oceanprof II sta. 68 (22°48'05"S, 40°06'38"W, 1,972 m).

## Etymology

*Brychios*, G. = deep, from the deep. Indicating that shells of this species were collected in the deeper localities among all species from Brazil. Adjective.

## Description

Shell trochiform, lenticular-discoid, spire depressed, wider than tall, 2.5 mm tall, 3.3



FIGS. 160–163. *Anatoma brychia*, n. sp., Paratype. MNRJ 26733, Holotype. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.



mm wide (holotype). Protoconch of  $\sim 0.8$  whorl, with scarce flocculent sculpture; weak apertural varix, not connected to embryonic cap, apertural margin straight. Teleoconch I of  $\sim 1.25$  whorls, almost smooth on initial 0.25 whorl, then with  $\sim 50$  thin axial cords, becoming evanescent before reaching suture above; interstices approximately three times width of cords, smooth; very thin spiral cord in position of selenizone, tending to disappear towards onset of teleoconch II, additional 1–2 spiral lines on second half of teleoconch I below position of selenizone. Teleoconch II up to 2.5 whorls, suture strongly impressed; first whorl with very faint sculpture; second whorl with slightly convex shoulder,  $\sim 70$  axial cords, reaching suture, proportionally increasing in strength with growth from thin to thick cords, not reaching edge of keel of selenizone; interspaces about three times width of cords; spiral cords thinner than axial cords, running over them, forming very slight thickenings at intersections, first spiral cord on shoulder at onset of teleoconch II,  $\sim 18$  on second whorl. Sutsel moderately high, approximately as wide as selenizone after first teleoconch II whorl. Base with faint constriction below selenizone, profile slightly rounded; axial ribs of same strength and density as on shoulder, reaching edge of keel of selenizone;  $\sim 20$  spiral cords, almost as strong as axial ribs, running over them, forming slightly thickening at intersections, extending onto keel of selenizone. Umbilicus wide, no funiculus. Aperture rounded, adumbilical portion strongly flared. Selenizone at periphery, wide; keels of moderate strength and elevation, somewhat adapically deflected; lunules distinct, not aligned to axial ribs on base, about one lunule to two axial ribs. Animal unknown.

#### Remarks

*Anatoma brychia* (Figs. 156–163) is the widest of all *Anatoma* species from Brazil, and has the largest teleoconch I of  $\sim 1.25$  whorls (Figs. 159, 163). Among all species studied by Geiger (2012), only *Anatoma boucheti* Geiger & Sasaki 2008, from Reunion island, has a similarly large teleoconch I (1.1 whorls); *Anatoma amoena* (Thiele, 1912), from Antarctica, has the largest with 2.33 whorls (Geiger, 2012).

The general shape of the shell of *A. brychia* is somewhat similar to *A. atlantica* (Figs. 77–94), but it is lower (Figs. 156, 160) and the sculpture is much weaker (Figs. 156–158, 160–162).

*Anatoma campense* (Figs. 148–155) has a similar aperture and deflected keel of the selenizone, but both can be distinguished by the weaker sculpture on shoulder of *A. brychia*, which has a lower sutsel and has a discoid shell shape, while *A. campense* is biconical.

Of all the species from Brazil with a spiral cord in the position of the selenizone on teleoconch I (*A. aedonia*, *A. atlantica*, *A. copiosa*, and *A. campense*), *A. brychia* has the thinnest one (Figs. 159, 163), and has the weakest sculpture on teleoconch I, which is almost smooth on the initial 0.25 whorl (Figs. 159, 163).

Some shells from off Georgia, U.S.A. (805 m) are somewhat similar to *A. brychia*, especially with respect to the thin sculpture and shell shape; its teleoconch I is long, but does not reach the 1.25 whorls as in *A. brychia*, and lacks the spiral cord in teleoconch I. Given such difference and the discrepancy in occurrence, we consider it as an unresolved record.

#### Distribution

U.S.A.: Georgia; Brazil: Rio de Janeiro; 1,068 m to 1,972 m.

*Anatoma* sp.  
(Figs. 164–167)

#### Material Examined

Brazil: Rio de Janeiro state: MNRJ 30525, [1].

#### Remarks

The only specimen available of this morphospecies is a somewhat broken shell. However, it can be recognized as different from all *Anatoma* species from the western Atlantic. The keel of selenizone is very damaged, but it seems to be wide, as can be seen close to aperture (Fig. 165), similar to *A. aedonia* (Figs. 6, 10, 14). The spiral sculpture on base and on teleoconch I are also similar to *A. aedonia*, but the general shell shape is very different, more globose and with a convex shoulder profile. This convex profile of the shoulder and the base is similar to *Anatoma weddelliana* (Zelaya & Geiger, 2007), from Antarctica, but in *Anatoma* sp. the sculpture is less dense and weaker. The strength and density of the sculpture is similar to *A. conica* (d'Orbigny, 1841) from subantarctic South America, but *A. conica* has a proportionally wider shell, has



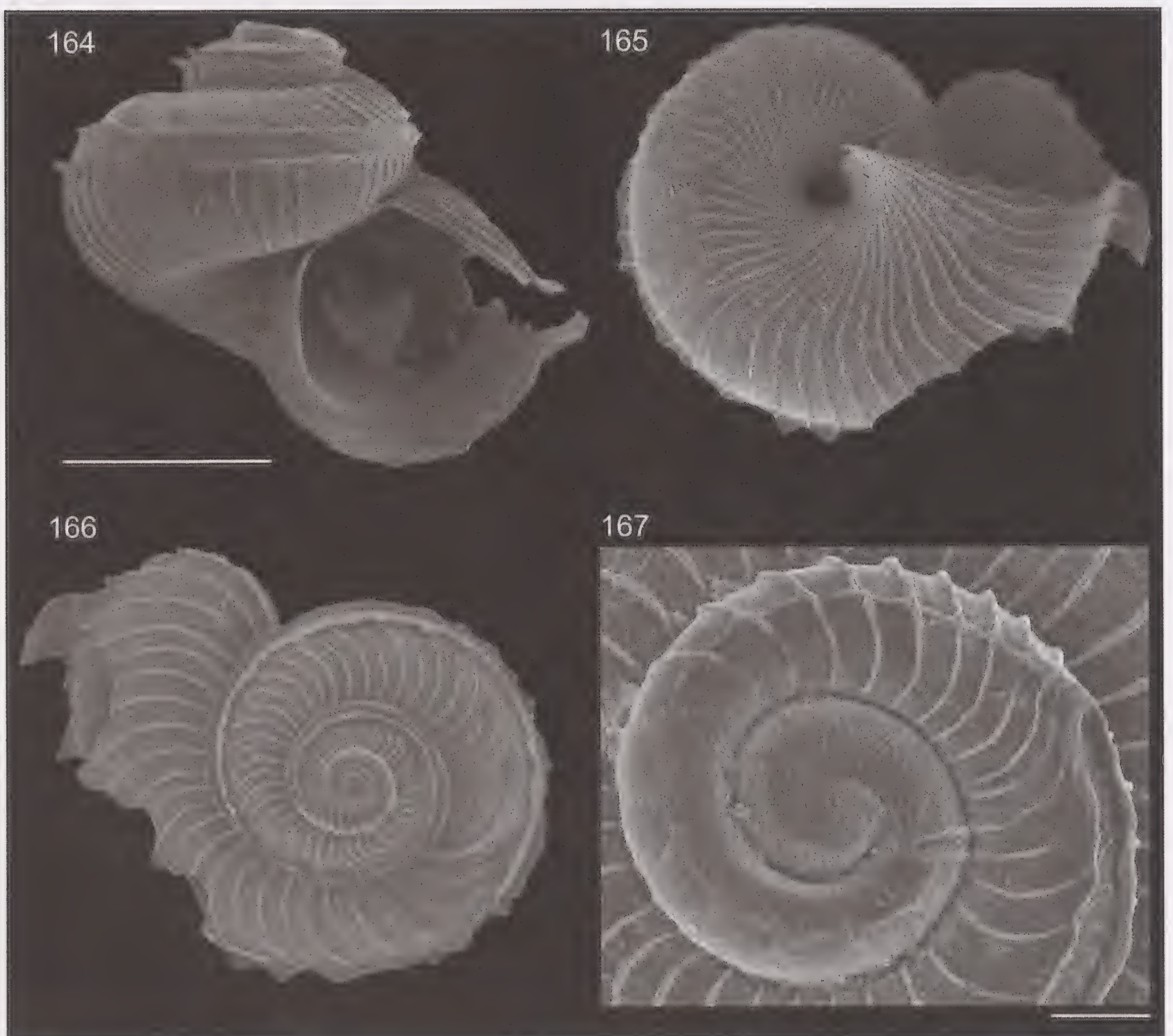
a shorter teleoconch I (0.5–0.66 whorl vs. 0.9) and lacks any trace of an apertural varix on the protoconch. *Anatoma finlayi* (Powell, 1937) from the Indian Ocean to the Central Pacific, *A. gunteri* (Cotton & Godfrey, 1933) from SE Australia, *A. indonesica* Bandel, 1998, from the Indo-Malayan Archipelago to the Western Pacific, and *A. janusa* Geiger, 2012, from the subtropical northeastern Atlantic all share the approximate strength and density of the sculpture on the shoulder, but have much weaker sculpture on the base.

## DISCUSSION

The present contribution adds a significant number of species in the genus *Anatoma* to

the South American fauna. It demonstrates that undescribed species are still being uncovered in taxa that have recently been monographed (Geiger, 2012). The main contributing factor is their relatively small size. Small specimens are not collected at all, are labor-intensive to sort, and taxonomic expertise for their identification is rarely available. Background information on already described species is mainly spread in the original literature, and many faunal inventories are rife with errors.

Monographs, such as Geiger (2012), are not exempt from errors either, as was predicted (Geiger, 2012: 68). Limited material of given taxa is the main culprit for such errors. The combination of local workers with access to material with global specialists on particular taxa has proven fruitful in the past (Geiger &



FIGS. 164–167. *Anatoma* sp. MNRJ 30525. Scale bars: whole shells = 1 mm, details = 100  $\mu$ m.



Jansen, 2004a, b; Geiger & Marshall, 2012; Sasaki et al., 2010; Zelaya & Geiger, 2007) and continues to make progress on the global taxonomic inventory.

Geiger & Sasaki (2009) demonstrated that even a well-studied area, such as Japan, still hides undescribed species of micromollusks; in Brazil, where the knowledge on diversity of micromollusks, especially from deeper localities, is far from complete, the same conclusion can be reached, on a larger scale. In spite of recent efforts to document diversity of micromollusks from Brazil in different families (e.g., Absalão, 2010; Fernandes et al., 2013; Pimenta et al., 2011; Simone & Cunha, 2014), a considerable amount of new species, as well as more accurate distribution range of already described species, is expected. In many cases, a simple examination of lots in collections of a given taxon of micromollusk can reveal that different species (including new ones) were lumped under a single specific name (e.g., Fernandes & Pimenta, 2011, for *Metaxia*).

In the particular cases of the Habitats and Oceanprof expeditions in Campos Basin, both in southeast Brazil, the samples are an important source for the discovery of new species of micromollusks, that are being continuously studied (e.g., Corrêa et al., 2014; 2014; Fernandes et al., 2015; Figueira & Absalão, 2010; Souza & Pimenta, 2014). Of special relevance in the case of the two above cited projects are the mesh sizes by which the samples were sieved: 0.3 mm (Oceanprof) and 0.5 mm (Habitats). Such mesh sizes contribute to the collection of very small specimens, including protoconchs of triphorids, ranging between 0.5 mm to 0.7 mm (pers. obs.). Geiger (2012) recommended 0.25 mm mesh size for all scissurellids; the smallest species being just slightly larger than 0.5 mm. Anatomids are generally larger, the smallest being still larger than 1 mm. Further details on collecting methods of micromollusks have been given elsewhere (Geiger et al., 2007). For most material already held in collections, details on collecting methods are usually not available.

In the case of *Anatoma*, since its description by Watson (1886), until very recently, *Anatoma aedonia* was considered the only species from Brazil (Rios, 1985, 1994, 2009). Now we have documented nine quite different species (Table 1).

With respect to the global faunistic regions used by Geiger (2012), the Argentinian, encompassing all Brazilian coasts, is represented now with ten *Anatoma* taxa (including *Anatoma*

sp.), a stark contrast to the two species previously listed (*A. aedonia* and *A. proxima*). The Argentinian province is now about as rich as the northeastern Atlantic (12 species), the Indian Ocean (11 species), New Zealand (11 species), and temperate Australia (nine species); only the Indo-Malayan area (28 species) and the Central Pacific (16 species) still exceed in terms of known *Anatoma* species.

The Anatomidae fauna from Brazil seems to have an affinity to that of the Caribbean/south U.S.A., with at least five species occurring from Florida to southeastern Brazil (Fig. 168). *Anatoma alternatisculpta*, previously known by its original description only, proved to be a very common species along the central coast of Brazil, with records along the seamounts of Vitória-Trindade sea chain. The occurrence of *Anatoma* in oceanic islands was also verified, with *A. aedonia* in São Pedro and São Paulo Archipelago, and *A. aedonia*, *A. americana* and *A. atlantica* on the slope of Abrolhos Archipelago.

The preferred depth distribution of Anatomidae on the upper continental slope has been confirmed. Shallow water species remain uncommon in this family, while true abyssal species remain rare due to extremely limited material. The deep, South American species *Anatoma argentinae* Zelaya & Geiger, 2007, may be more widely distributed, but seems to be restricted to abyssal depths. It was not recovered in any of the Brazilian bathyal samples, where the deepest species up to now, is *Anatoma brychia* (1,972 m). Considering the bathymetric distribution of the species along the Brazilian coast, *A. campense* and *A. brychia* are restricted to bathyal depths and *A. copiosa*, *A. alternatisculpta*, *A. espirito-santense* and *A. americana* are encountered over a somewhat wider depth range on the continental shelf (ranging from ~ 50 m to ~ 160 m) and upper slope (not beyond 230 m), with a single occurrence of *A. americana* in ~ 940 m in the Abrolhos Archipelago. *Anatoma aedonia*, *A. proxima* and *A. atlantica*, on the other hand, are found over a wide bathymetric range, from the continental shelf to around 700 m to 1,000 m on the continental slope.

As a result of recent great efforts of environmental characterization of the Campos Basin, a strategic area for oil exploration in southeastern Brazil, a large amount of biological material is available for taxonomic study. This may explain the occurrence of several species in this sedimentary basin, where the continental shelf (its breaking ~ 110 m) and upper slope (up to



TABLE 1. Comparative shell morphology of *Anatoma* species occurring in Brazil.

| Species                                      | <i>Anatoma aedonia</i>                                | <i>Anatoma proxima</i>                                                                                   | <i>Anatoma americana</i>                                       | <i>Anatoma ternatisculpta</i>          | <i>Anatoma atlantica</i>                                         | <i>Anatoma copiosa</i>                                            | <i>Anatoma piritosantense</i>                                                     | <i>Anatoma campense</i>                       | <i>Anatoma brychia</i>                              | <i>Anatoma</i> sp.        |
|----------------------------------------------|-------------------------------------------------------|----------------------------------------------------------------------------------------------------------|----------------------------------------------------------------|----------------------------------------|------------------------------------------------------------------|-------------------------------------------------------------------|-----------------------------------------------------------------------------------|-----------------------------------------------|-----------------------------------------------------|---------------------------|
| Shell shape                                  | trochiform, spire turreted                            | trochiform, spire turreted                                                                               | trochiform- len- ticular, spire slightly turreted to depressed | len- ticular- discoid, spire depressed | len- ticular- discoid, spire depressed                           | len- ticular- discoid, spire depressed                            | trochiform- globose, spire turreted                                               | trochiform, spire turreted-conical            | len- ticular- discoid, spire depressed              | trochiform                |
| No. of proto- conch whorls and sculp- ture   | 0.8, flocculent (scarce)                              | 0.8, flocculent (scarce)                                                                                 | 0.8, flocculent (scarce) with spiral line of granules          | 0.8, flocculent (very scarce)          | 0.8, flocculent (very scarce), with a faint spiral line          | 0.8, flocculent (very scarce), with a faint spiral line           | 0.8, much erod- ed in all shells, some irregular granules visible in some regions | 0.8, flocculent (scarce)                      | 0.8, flocculent (dense)                             | flocculent (dense)        |
| No. of teleo- conch I whorls                 | ~ 1.0                                                 | ~ 0.6                                                                                                    | ~ 0.5                                                          | ~ 0.75                                 | ~ 0.75                                                           | ~ 0.75                                                            | ~ 0.6                                                                             | ~ 1.0                                         | ~ 1.25                                              | ~ 0.9                     |
| Spiral cord on teleo- conch I                | always present, strong, reaching margin of selenizone | absent                                                                                                   | absent                                                         | absent                                 | variable, when present, strong and reaching margin of selenizone | always present, becoming evanescent, towards margin of selenizone | absent                                                                            | always present, reaching margin of selenizone | always present, thin, reaching margin of selenizone | present                   |
| No. and type of axial ribs on teleo- conch I | ~ 30, reaching upper suture                           | ~ 40, some reaching upper suture, some stopping short of it, intercalated and sometimes merging in pairs | ~ 30, some upper suture                                        | ~ 25, reaching upper suture            | ~ 30, reaching upper suture                                      | ~ 25, reaching upper suture                                       | ~ 12, reaching upper suture                                                       | ~ 40, reaching upper suture                   | ~ 50, not reaching upper suture                     | 17, reaching upper suture |
| Sculpture on teleoconch I interspaces        | smooth                                                | irregularly granulated                                                                                   | irregularly granulated                                         | irregular concretions                  | smooth or with irregular concretions                             | smooth                                                            | irregular concretions                                                             | smooth                                        | smooth                                              | smooth                    |

(continues)



(continued)

| Species                                                                 | <i>Anatoma aedonia</i>                                          | <i>Anatoma proxima</i>                                            | <i>Anatoma americana</i>                                                                                  | <i>Anatoma tematisculpta</i>                                         | <i>Anatoma atlantica</i>                                        | <i>Anatoma copiosa</i>                                                  | <i>Anatoma piritosantense</i>                                             | <i>Anatoma campense</i>                                                         | <i>Anatoma brychia</i>                                                 | <i>Anatoma</i> sp.                                              |
|-------------------------------------------------------------------------|-----------------------------------------------------------------|-------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------|-----------------------------------------------------------------|-------------------------------------------------------------------------|---------------------------------------------------------------------------|---------------------------------------------------------------------------------|------------------------------------------------------------------------|-----------------------------------------------------------------|
| No. and type of axial ribs on shoulder of Second whorl of teleoconch II | ~ 50, reaching suture                                           | ~ 55 to ~ 90, usually reaching suture, uncommonly not reaching it | ~ 120, alternating pattern of reaching suture and stopping short of it, sometimes merging close to suture | ~ 35 to 45, reaching suture                                          | ~ 100, reaching suture                                          | ~ 120, reaching suture                                                  | ~ 65, reaching suture, with irregular interspaces                         | ~ 80, reaching suture                                                           | ~ 70, reaching suture                                                  | ~ 38, reaching suture                                           |
| Axial ribs on keel of selenizone                                        | strongly projected on ad and abapically portions, reaching edge | strongly projected on ad and abapically portions, reaching edge   | variably projected on adapical portion, strongly projected abapically, reaching edge abapically           | very variable projected on ad and abapically, variably reaching edge | strongly projected on ad and abapically portions, reaching edge | very faint, not reaching edge                                           | strongly projected on ad and abapically portions, partially reaching edge | strongly projected on abapically portions, not reaching edge of only abapically | projected on abapically portions, not reaching edge of only abapically | strongly projected on ad and abapically portions, reaching edge |
| No. of spiral cords on shoulder of second whorl of teleoconch II        | 2 to 5                                                          | 6 to 8                                                            | ~ 15                                                                                                      | very variable, ~ 15 to ~ 10                                          | ~ 15                                                            | ~ 8                                                                     | ~ 10                                                                      | ~ 10                                                                            | ~ 18                                                                   | 10                                                              |
| Sutsel height on spire                                                  | high                                                            | high                                                              | variably high                                                                                             | very low                                                             | variably low                                                    | very low                                                                | high                                                                      | high                                                                            | low                                                                    | high                                                            |
| Sculpture on base                                                       | ~ 15 spiral cords; ~ 40 axial cords well spaced                 | ~ 20 spiral cords; ~ 100 axial ribs                               | ~ 24 spiral cords; ~ 140 axial ribs very closed spaced                                                    | ~ 15 spiral cords; ~ 80 axial ribs variable in strength              | ~ 25 spiral cords; ~ 130 axial ribs                             | ~ 15 spiral cords, stronger than axial ribs which are like growth lines | ~ 30 spiral cords; ~ 75 axial ribs regularly spaced                       | ~ 25 spiral cords almost inconspicuous; ~ 90 axial ribs very close together     | ~ 20 spiral cords; ~ 95 axial ribs                                     | 10                                                              |



550 m) are characterized by a heterogeneous substratum of fine to coarse sand intercalated with calcareous banks (Viana et al., 1998; Lavrado et al., 2010). Middle (up to 1,200 m) and lower slope (beyond 1,200 m) are predominantly composed of fine mud. In this region, *A. proxima*, *A. americana*, *A. alternatisculpta* and *A. copiosa* are relatively abundant on the shelf break/upper slope, while *A. campense* and *A. brychia* are less common, occurring on mud bottoms of the middle/lower slope. These data are in accordance with Geiger's (2012) inference that Anatomidae live on soft substrates.

In spite of the large amount of specimens collected by those recent expeditions, com-

plete ones, i.e. specimens with the soft parts preserved are very rare, with only three species being represented; this is in broad accordance to the material listed in Geiger (2012), in which around 30% of the 79 species studied are represented in collections by complete specimens, indicating the difficulty in collecting live specimens in this group.

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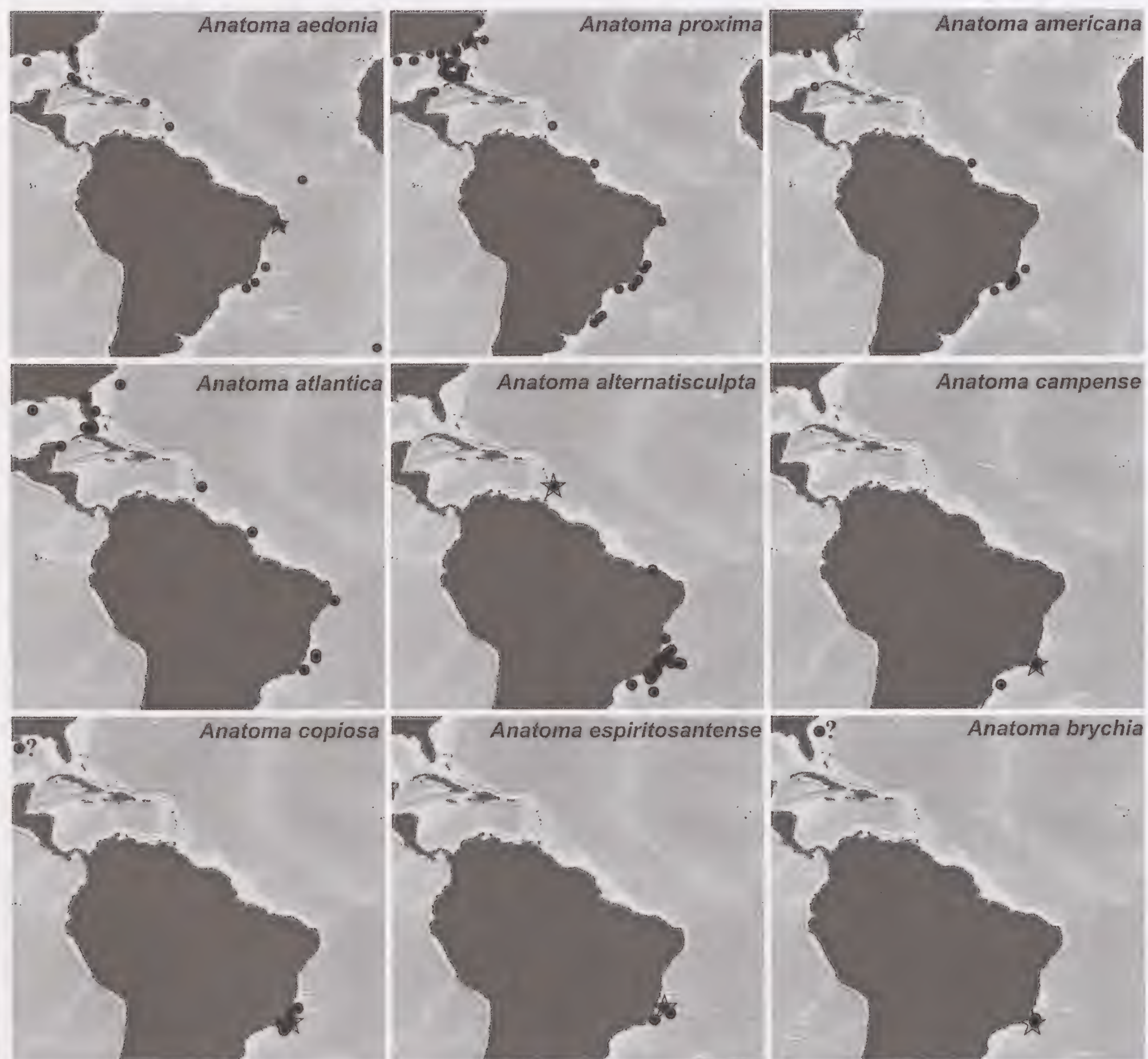


FIG. 168. Distribution of *Anatoma* species from Brazil in the western Atlantic. White star: type locality; black dot: specimen record; black square: imprecise type locality; ?: doubtful record.



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## INTER-POPULATION DIFFERENCES AND SEASONAL DYNAMIC OF THE BACTERIAL GUT COMMUNITY IN THE ENDANGERED LAND SNAIL *HELIX POMATIA* (GASTROPODA: HELICIDAE)

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### ABSTRACT

Among the multifaceted environmental factors, the bacterial community ingested with soil and food might play an important role in physiological processes of terrestrial gastropods, with consequences on population dynamics and species distribution patterns. Therefore, we investigated the bacterial gut community structure and seasonal dynamic in three populations of the protected endangered land snail *Helix pomatia*. The PCR-DGGE fingerprinting analysis followed by Nonmetric Multidimensional Scaling (NMDS) showed that Gamma- and Alphaproteobacteria were common to all populations, while Mollicutes and Betaproteobacteria were population specific. Allochthonous strains might be transiently abundant in the gut of foraging snails with respect to habitat conditions. Autochthonous strains were permanently present in the gut, even after expulsion of the gut content at hibernation beginning. Some of these permanent strains are known to have ice-nucleating activity, which is consistent with the limited cold hardiness in this species. Snails that did not enter hibernation despite being exposed to winter conditions had a poor bacterial community. In conclusion, the bacterial community structure differed between habitats and physiological states, and might be important for physiological processes and survival. Further studies should focus on the individual variation in bacterial community and investigate how it is affected by environmental changes.

Key words: digestive gland, hibernation, ice nucleating bacteria, 16S rDNA bands, proximal intestine, distal intestine, soil invertebrate; PCR-DGGE.

### INTRODUCTION

In temperate areas, terrestrial mollusks have to cope with contrasting climatic situations during the year and are exposed directly to fluctuating soil properties. Among the multifaceted biotic and abiotic factors in the habitat, the bacterial community ingested with soil and vegetal food might play an important role in physiological processes of terrestrial gastropods (Knapp et al., 2009a, b) with consequences on population dynamic and species distribution. Understanding these small-scale physiological processes is the basis for a large-scale physiological perspective that could provide insights in species distribution patterns (Chown & Gaston, 2008).

The edible land snail *Helix pomatia* (Linnaeus, 1758) is endangered in Germany (§1 Abs.1 BArtSchV), suffering from habitat destruction (hedges and skirts of the forest)

by intensive land use and exposure to toxic substances (Dallinger et al., 2001). The species is protected in Europe since 2002 by Appendix III of the Bern Convention, and standing to benefit from a general collection interdiction in Germany since 2005 (§42 Abs. 1 Nr. 1 BNatSchG). Protection measures in Germany include promoting snail farming and lowering habitat disturbance, both requiring studies about crucial life stages in order to limit mortality in the species artificial and natural habitat. This species has a large latitudinal (Greece to Sweden) and longitudinal (France to Poland) distribution in Europe (Nietzke, 1970), exposing individuals to a wide range of different altitudes, habitats, climatic situations and annual variations. Mortality during hibernation seems to be the key factor of population dynamic in *Helix pomatia* (Tischler, 1973; Lind, 1988) and in other Helicidae of Europe (Peake, 1978;

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Cain, 1983). The bacterial gut community of snails is likely to be involved in a wide range of physiological processes related to digestion and cold hardiness during hibernation (Flari & Charrier, 1992; Ansart et al., 2010; Cardoso et al., 2012a, b), and subsequently to maintenance and survival.

In earlier studies on cultivable intestinal bacteria of *Helix pomatia* and *Cornu aspersum* (Charrier et al., 1998; Kiebre-Toe et al., 2003; Charrier et al., 2006), facultative anaerobes species appeared to be dominant: *Citrobacter* sp., *Enterobacter* sp., and *Klebsiella* sp., which is in accordance with the existence of microoxic regions in the vicinity of the apical epithelium of the anoxic gut (Charrier & Brune, 2003). Most of the cultivated strains from Enterobacteriaceae as well as *Lactococcus* sp. and *Clostridium* sp. were also found in environmental samples and food products (Olsson et al., 2004; Charrier et al., 2006). Despite some Enterobacteriaceae and Enterococcaceae that have their natural niche in the enteric environment of snails (e.g., *Buttiauxella* sp. and *Kluyvera* sp.; Muller et al., 1996), the majority of the bacterial flora of Helicidae intestine seems to be exogenous, ingested with food and faeces as well as by scraping the soil, the latter being especially the case in newly hatched snails (Charrier, 1990; Watkins & Simkiss, 1990). In hibernation, the bacterial gut flora undergoes changes when exogenous species are not provided, while some bacteria species are nourished by mucus secretions (Jeuniaux, 1955; Pereira & Breckenridge, 1981).

We investigated the bacterial community structure of the gut in activity and hibernation in three geographically distinct populations of *Helix pomatia* to get a better picture of the role of bacteria in the functional ecology of terrestrial gastropods. This study is designed to present a first characterization of inter-population differences, which is essential for addressing further questions related to climate adaptation and evolution in different habitats and geographic regions. We investigated the bacterial community structure in activity and hibernation in order to better understand the origin of bacterial flora and its seasonal dynamic. We hypothesize that (i) the initiation of hibernation accompanied by gut clearance might provoke changes in the bacterial community structure in the intestinal tract of *Helix pomatia*, and that (ii) the bacterial community structure of active snails differs between populations of different geographic origins according to habitat and climate differences, but the same endogenous flora persists during hibernation whichever population origin.

## MATERIAL AND METHODS

### Sampling of *Helix pomatia* and Hibernation Acclimatisation

In September 2006, 50 adult snails were collected (authorisation §2 Abs. 2 BNatSchG from September 18, 2005) in three geographically distant forest habitats with different mean air temperatures (Fig. 1). Population IT: 15 snails collected in the forest (dominated by *Carpinus betulus* and *Quercus robur* with ground vegetation dominated by *Stellaria holostea*, *Hedera helix*, *Rubus fruticosus* and *Lonicera periclymenum*) near Cherasco, region of Piemonte in Italy (44°65'19"N, 7°84'05"E, 200 m a.s.l.). Population RHE: 20 snails collected in the forest (dominated by *Carpinus betulus* and *Robinia pseudoacacia* with ground vegetation dominated by *Urtica dioica*, *Impatiens non-tangere*, *Geranium robertianum*, *Galeopsis tetrahit*, *Ranunculus ficaria*, *Chelidonium majus*, and *Fragaria vesca*) near Grünstadt-Asselheim, Rhine valley in Germany (49°33'14"N, 8°9'46"E, 150 m a.s.l.). Population ALB: 15 snails collected in the forest (dominated by *Fagus sylvatica* and *Alnus glutinosa* with ground vegetation dominated by *Urtica dioica*, *Fumaria officinalis*, *Impatiens non-tangere*, *Geranium robertianum*, *Viola reichenbachiana*, *Anemone nemoros*, *Dentaria bulbifera*) near Weiler-Indelhausen, mountains Schwäbische Alb in Germany (48°18'7"N, 9°29'47"E, 800 m a.s.l.). The maximal shell breadth of snails (Mean  $\pm$  SE) is different between RHE (40.79  $\pm$  0.74 mm) and ALB (38.07  $\pm$  0.71 mm), but not compared to IT (40.20  $\pm$  0.72 mm, ANOVA,  $F_{2,27} = 3.74$ ,  $P = 0.04$ ,  $N_{RHE} = N_{ALB} = N_{IT} = 10$ ).

Directly after collection, five snails of each population were starved for one day in order to empty the gut of food particles, then sacrificed and stored at -80°C (active snails: sample A). Because it is difficult to collect snails in hibernation conditions (frozen soil, unknown location of burial), five further snails of each population were progressively acclimated to hibernation condition in the laboratory (temperature 5  $\pm$  1°C, relative humidity: 50%, 24 h darkness) over two weeks (decrease of 2°C/2 days and 10%/3 days) without feeding. By the end of the second week, snails obturated the peristome of their body shell with a hard calcified epiphragm, thereby initiating hibernation. After three months of hibernation, snails were sacrificed and stored at -80°C (hibernating snails: sample H). In order to follow



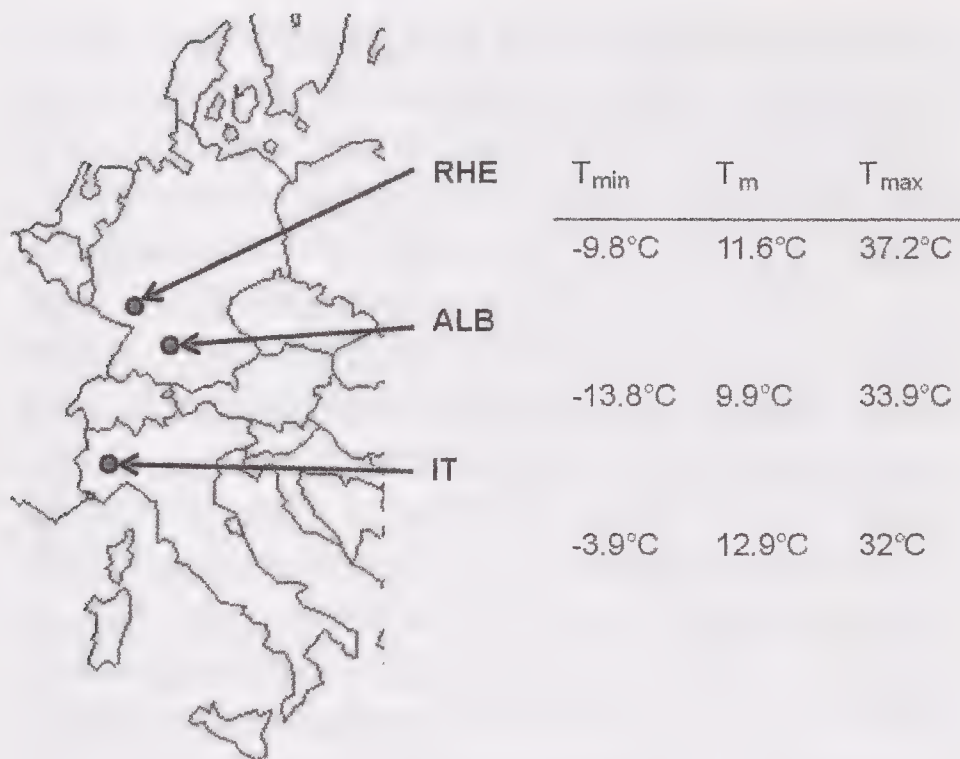


FIG. 1. Locations of the three *Helix pomatia* populations with temperature for the sampling year (<http://www.ilmeteo.it> and <http://www.dwd.de>). ALB Schwäbische Alb in Germany, RHE: Rhein valley in Germany, and IT: Cherasco, Piemont in Italy).  $T_{\min}$  – minimal temperature,  $T_m$  – mean temperature,  $T_{\max}$  – maximal temperature.

the dynamic changes of bacterial community through entry into hibernation, we transferred supplementary snails of the RHE population to hibernation conditions (temperature  $5 \pm 1^\circ\text{C}$ , relative humidity: 50%, 24 h darkness). For this population, besides the sample H, we sacrificed five of them right after epiphragm finalization (hibernation beginning sample: Hb) and five of them without epiphragm, but inactive for 2 weeks in hibernation conditions with a deeply withdrawn body in the shell cavity (non hibernating sample: nH). Such non-hibernating snails could generally be observed in natural conditions (Nietzke, 1970; Kiliyas, 1985) and occurred also in the ALB and IT sample (two and one snails, respectively). These snails do not produce an epiphragm and do not initiate hibernation, which is usually accompanied by the rapid death in early winter.

#### DNA Extraction, PCR-DGGE and Sequencing

In this first descriptive study, we focused on the most dominant bacterial phylotypes at population level using the technique of PCR-DGGE on a pooled sample of five individuals of each snail population. All snails were surface-sterilized with ethanol (70%) and dissected on a sterile workbench. The digestive tract was extracted and separated in three parts: the proximal intestine (PI), the distal intestine (DI) and the digestive gland (DG). For DNA extrac-

tion, we pooled tissues of the five individuals of each sample (fresh mass of tissue pool: PI = 0.25 g, DI = 0.5 g, and DG = 1 g) and homogenized the pool using sterile Circonium beads in a bead-beating step (2 min, 30 Hz, Retsch MM2000, USA). After addition of 650  $\mu\text{l}$  CTAB 2% (in 1 M TrisHCl pH 8, 5 M NaCl and 0.5 M EDTA) and 20  $\mu\text{l}$  Proteinase K (20 mg/ml), followed by bead-beating, the homogenate was incubated for 1 h at  $65^\circ\text{C}$  (Polystat, Bioblock Scientific, France) and then centrifuged (14000 g, 2 min,  $4^\circ\text{C}$ , Sigma® 3K 12, Fisher Bioblock Scientific, France). To the supernatant were added 600  $\mu\text{l}$  of phenol:chlorophorm:isoamyl alcohol (25:24:1, v/v) and slightly shaken for 5 min. After centrifugation (14000 g, 4 min,  $4^\circ\text{C}$ ), the supernatant was mixed with 600  $\mu\text{l}$  chloroform and centrifuged again (14000 g, 10 min,  $4^\circ\text{C}$ ). The supernatant was then added to a twofold volume of isopropanol in order to precipitate the DNA. After 1.5 h at  $-20^\circ\text{C}$  and a centrifugation (14000 g, 30 min,  $4^\circ\text{C}$ ), DNA was washed with 500  $\mu\text{l}$  cooled ethanol (70%) and centrifuged again (14000 g, 15 min,  $4^\circ\text{C}$ ). Extracted DNA was then dried at ambient temperature for 30–40 min before adding TE buffer (10 mM Tris pH 7.6, 1 mM EDTA pH 8) and purifying twice using the Kit MicroSpin S-400 HR (Bioscience, UK) according to the manufacturer's protocol. DNA yield and quality was assessed by concentration measurements using NanoDrop® (NanoDrop Technologies, DE, USA), and subsequently a twofold dilution was performed.

Extracted DNA was amplified in a PCR thermocycler (Mastercycler personal Eppendorf®, USA) with a general primer, the 16S rDNA primer set 518-r (ATT-ACC-GCG-GCT-GCT-GG) and the GC-clump primer gc-338-f (CGC-CCG-CCG-CGC-GCG-GGC-GGC-GGC-GCG-GGG-GCA-CGG-GGG-GAC-TCC-TAC-GGG-AGG-CAG-CAG). Each PCR mixture of 25  $\mu\text{l}$  contained one unit of DNA polymerase-dNTP mix puReTaq Ready-to-go PCR bead (illustra™, GE Healthcare, UK), 0.1  $\mu\text{g}$  of extracted DNA, and 0.25  $\mu\text{M}$  of each primer. The PCR included an initial 5 min denaturation at  $94^\circ\text{C}$  and was followed by 35 thermal cycles of 0.5 min at  $94^\circ\text{C}$ , 0.75 min at  $55^\circ\text{C}$  and 1.5 min at  $72^\circ\text{C}$ . Amplification was completed with a final extension step at  $72^\circ\text{C}$  for 20 min. PCR products were verified by electrophoresis 2% (w/v) agarose gels (55 min, 100 V) and ethidium bromide staining (10 mg.ml<sup>-1</sup>) using the molecular marker Ladder (Invitrogen, France).



For DGGE (Dcode System, BioRad, Canada), 2 µl PCR product was loaded onto 8% (w/v) polyacrylamide gels with denaturing gradient of 40–55% (100% denaturant according to 7 M urea plus 40% formamide in 50X TAE buffer) and was run 15 h at 75 V and 60°C in 0.5X TAE buffer (20 mM Tris, 10 mM Acetate, 0.5 mM EDTA pH 7.6). After electrophoresis, the gel was stained with ethidium bromide (10 mg.ml<sup>-1</sup>) and scanned using UV (Transilluminator HOOD, BioRad, Canada with camera Canon CCIR). The DGGE gels were repeated once to verify for reproducibility which was 100%.

DGGE banding patterns were normalized and analyzed using the software Quantity One (BioRad, Canada). DNA bands (two replicates maximal per line on the gel) were excised from the gel and incubated 12 h in 25 µl TE buffer at 5°C. In order to purify the excised DNA bands, 2 µl of eluted DNA in sterile TE buffer were used for PCR with the same primer set and the same cycle, followed by DGGE in the same conditions as described above. Excision of the selected bands, PCR and DGGE on the excised bands were repeated again before a final twofold PCR on the purified excised DNA bands. The PCR amplicons were used for sequencing (COGENICS, Takeley, UK), and 18 bacterial nucleotide sequences were submitted to GenBank database (Accession numbers KP122319-KP122336).

### Data Analysis

In order to detect differences of band patterns between population samples, the nonmetric multidimensional scaling method (NMDS) with Jaccard similarity coefficient was applied to presence/absence data determined for each band and based on the normalized minimal threshold density (Legendre & Legendre, 2007; Ramette, 2007). The stress coefficient indicates the badness-of-fit, this is the quality of the NMDS ( $S < 0.20$ : acceptable). Distances between points (corresponding to each gut compartment) were calculated with the equation  $d_{ij} = ((x_i - x_j)^2 + (y_i - y_j)^2)^{0.5}$ , where  $d_{ij}$  is the distances between two points  $i$  and  $j$ , and  $x$  and  $y$  are the scores on the first and the second axis, respectively. According to Okubo & Sugiyama (2009), the Kruskal-Wallis test was used on scores of the first and second axes and on distances to analyse bacterial community differences. All analyses were conducted with the software R 2.8.0 (R Core Team, 2008).

All sequences with all nucleotides were aligned with the software BioEdit Sequence Alignment Editor 7.0.9.0 (Hall, 1999) using ClustalW (Thompson et al., 1994) and compared to those found in the GenBank database (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>). Only results with the highest E-value have been retained and phylogenetic affiliation was analysed with the Neighbour Joining method using the software MEGA 4.1 (Tamura et al., 2007). The consistency of the unrooted tree was validated by bootstrapping ( $N = 1000$ ). The taxonomic hierarchy of the sequences was determined using the RDP classifier tool (<http://rdp.cme.msu.edu/index.jsp>; Wang et al., 2007) with a bootstrap cutoff of 50% since bands were  $< 250$  pb (Claesson et al., 2009).

## RESULTS

### Bacterial Gut Community Structure as a Function of Seasonal Conditions and Geographic Origin

The DGGE profiles allowed us to gain insights in the structural composition of dominant strains (Claesson et al., 2009) in the bacteria community of the compartmentalized gut of the land snail *Helix pomatia*. A comparative study of different fingerprinting methods had shown, that DGGE gives the clearest discrimination among microbiota communities (Okubo & Sugiyama, 2009), and was applied to a wide range of questions in the context of community structure and dynamic (e. g., Brunvold et al., 2007; Sandaa et al., 1999, 2003; Knapp et al., 2009a, b).

In general, band number in gut compartments of population samples reached from 4 to 16 bands (Fig. 2). Bacterial gut communities were also clearly discriminated on the first axis of NMDS with an acceptable stress coefficient (Fig. 3). Furthermore, the bacterial communities of the three studied populations were not only separated in activity conditions (Kruskal-Wallis test,  $H_2 = 7.2$ ,  $P = 0.027$ ), but also in the hibernation conditions (Kruskal-Wallis test,  $H_2 = 6.49$ ,  $P = 0.039$ ), on the first axis.

The excised bands could be successfully purified and sequenced, corresponding to ba1–ba16 (Fig. 2). Several bands appeared not to be of bacterial origin after alignment in the GenBank database (snail and plant DNA) and were discarded from further community or taxonomic analysis. Most of the excised



16S rDNA sequences were closely related to sequences from Pseudomonadaceae, Enterobacteriaceae, Xanthomonadaceae and Sphingomonadaceae with a similarity  $\geq 98\%$  (Fig. 4). The similarity of ba9.2 with *Lactococcus lactis* was only 86% and of ba8 with *Mycoplasma bovirhinsis* only 92%, as well as the similarity of some bands (ba1, ba2, ba9.1, ba12, ba13) with sequences of unknown bacteria or other DGGE bands ranged from 90 to 94%. The taxonomic affiliation of unknown GenBank sequences and bands could be determined with the RDP classifier tool, revealing an affiliation to the genus of *Variovorax* sp. for ba6, to the class Alphaproteobacteria for ba1 and ba9.1, and to the Phylum Firmicutes for ba2. The bands ba12 and ba13 could not be classified due to poor sequencing quality. The closest relatives in the GenBank database were of the genus *Pantoea* sp. for ba11.2, ba14, and ba16, *Flavimonas* sp. for ba5, and *Sphingopyxis* sp. for ba15, while the same bands and sequences from the GenBank were classified to the genus *Buttiauxella* sp., the genus *Pseudomonas* sp., and the family Erythrobacteraceae, respectively, by the RDP classifier tool. The closest relatives from the

alignment in GenBank database for ba1 and ba9 were assigned to the genus *Caulobacter* sp. and to the class of Alphaproteobacteria, respectively.

Gammaproteobacteria and Alphaproteobacteria were the most abundant classes in snail guts of all populations (Fig. 5). However, among Alphaproteobacteria IT population lacked Pseudomonadaceae, and Xanthomonadaceae were only found in RHE population. Betaproteobacteria (Comamonadaceae) were only present in ALB population in activity condition, and Mollicutes were specific of RHE and IT population. One phylotype of Firmicutes appeared only in hibernation conditions of all populations, the other only in the RHE population, in activity.

#### Bacterial Community Structure in the Compartmentalized Gut for Different Physiological States

In the DGGE profile of RHE snails at the beginning of hibernation and in non-hibernating snails (Fig. 6) we could identify the same sequences of 16S rDNA bands by alignment with the sequences of the DGGE in Figure

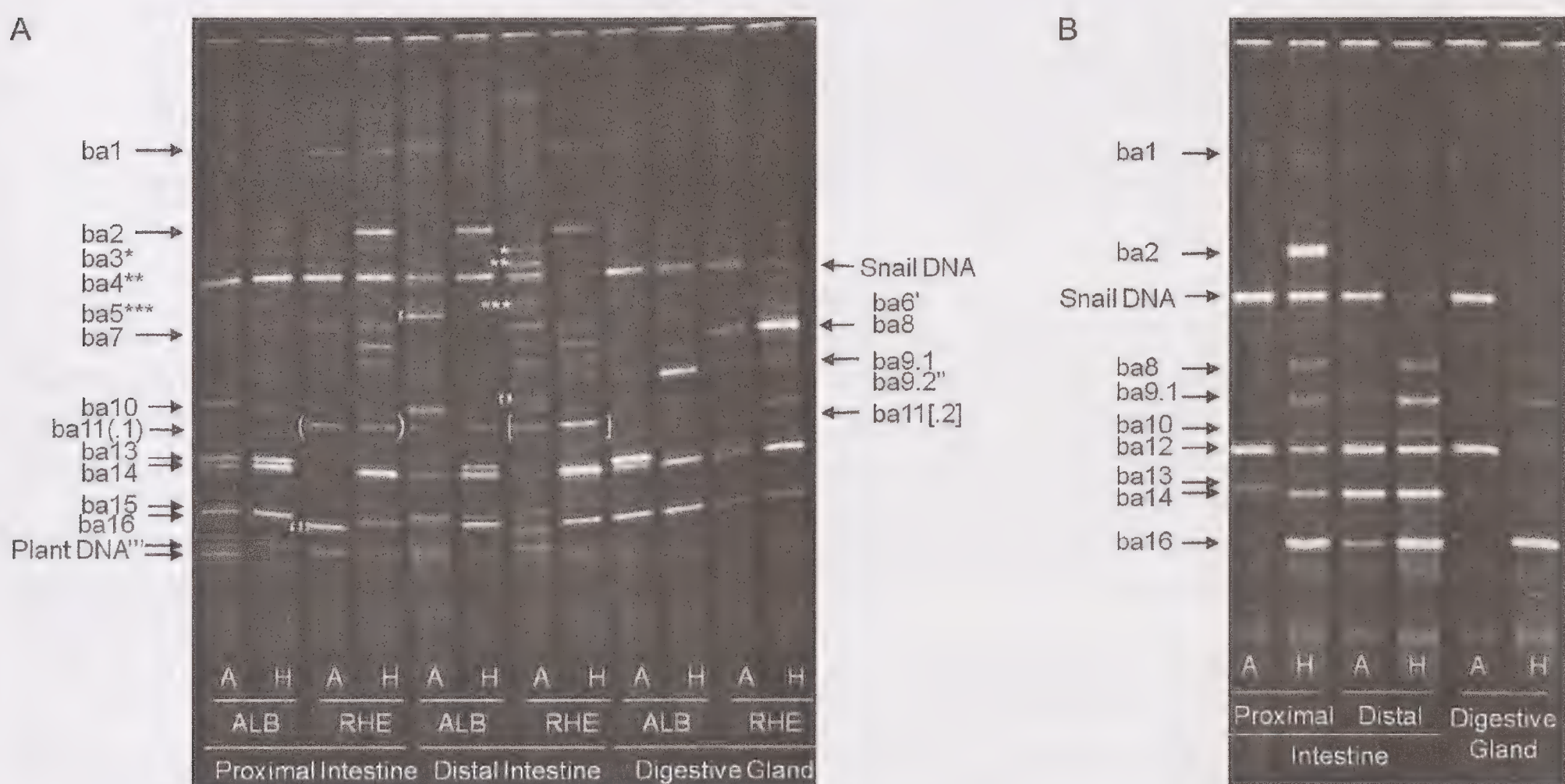


FIG. 2. Fingerprints of the bacterial community in each gut compartment of different populations of *Helix pomatia* in different conditions (activity: A, and hibernation: H). FIG. 2A: Schwäbische Alb (ALB) and Rhein valley (RHE) in Germany; FIG 2B: Italy. Two bands were sequenced in those lines of 16S rDNA bands, which are indicated by ba1 to ba16. Apostrophes and asterix indicate single bands. Brackets and parantheses indicate bands occurring only in two conditions within the same gut compartment of the same population. Several bands revealed to be not of bacterial origin after alignment in GenBank (snail and plant DNA).



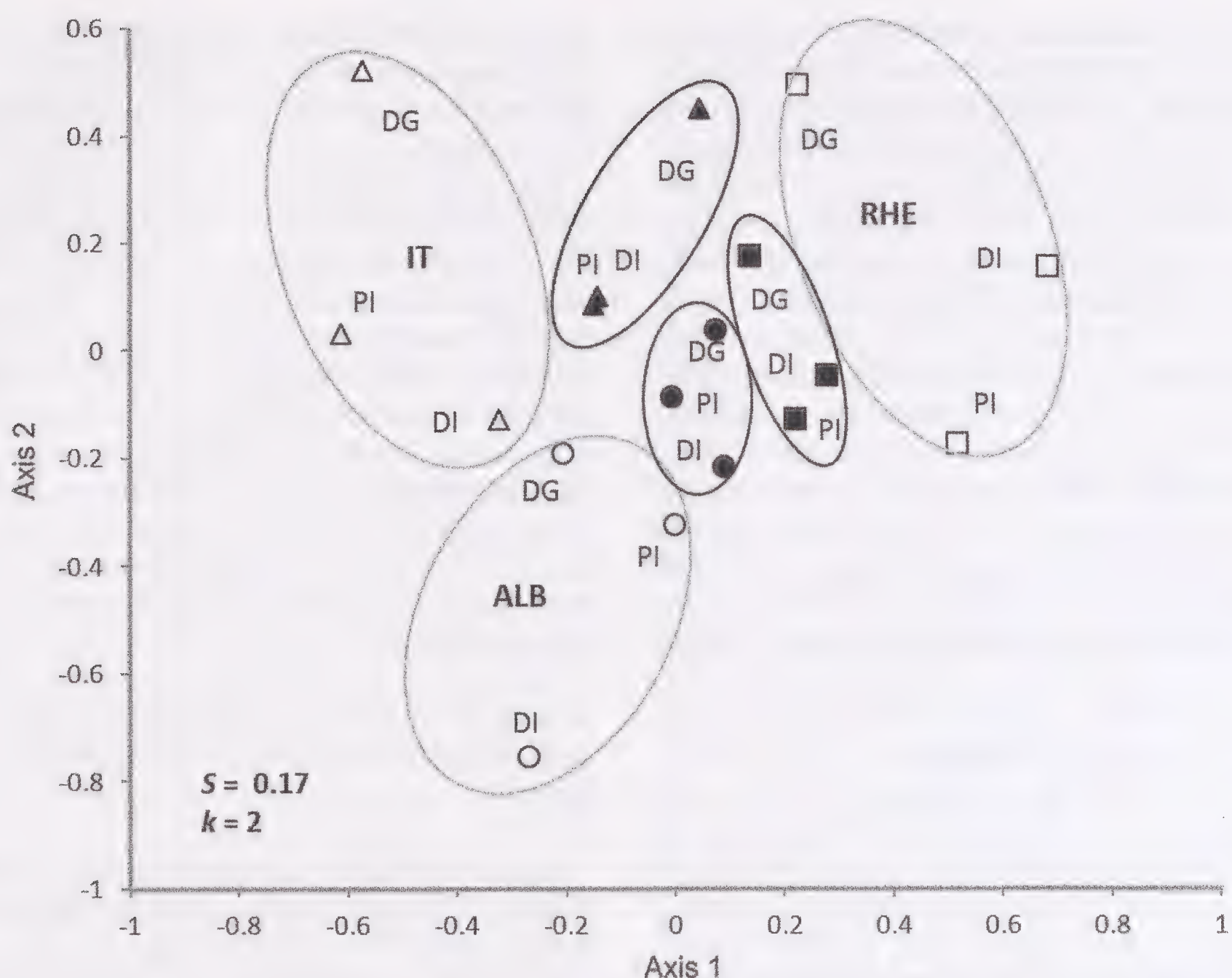


FIG. 3. NMDS plot of bacterial DGGE fingerprinting patterns in different populations (Schwäbische Alb in Germany – ALB: circles, Rhein valley in Germany – RHE: squares, and Italy – IT: triangles) and different conditions (activity – A: open symbols, hibernation – H: black symbols) based on extracted 16S rDNA from the content of different compartments of the digestive tract (proximal intestine: PI, distal intestine: DI, digestive gland: DG) in the land snail *Helix pomatia*.  $S$  indicates the stress and  $k$  the total number of axes used in the analysis. Kruskal-Wallis test of scores between samples on the 1<sup>st</sup> axis:  $H = 15.50$ ,  $DF = 5$ ,  $N = 18$ ,  $P = 0.0084$ , and on the 2<sup>nd</sup> axis:  $H = 8.81$ ,  $DF = 5$ ,  $N = 18$ ,  $P = 0.12$ .

2. The band patterns of DGGE fingerprinting of all physiological states in RHE population showed a significant discrimination of bacterial community structure on the second axis in the NMDS plot with an acceptable stress coefficient (Fig. 7). Non hibernating snails showed the most dissimilar bacterial community structure.

As already observable in the NMDS plot of the three populations (Fig. 3), the different compartments of the digestive tract were well distanced from each other in activity on the NMDS plot, but approached each other in hibernation (A versus H, Kruskal-Wallis test,  $H_1 = 7.75$ ,  $DF = 1$ ,  $N = 18$ ,  $P = 0.005$ ). In the NMDS plot of the RHE population (Fig. 7), hibernating and non-hibernating snails of the RHE population showed comparable distances between gut compartments (H versus nH, Kruskal-Wallis

test,  $H = 0.43$ ,  $DF = 1$ ,  $N = 6$ ,  $P = 0.51$ ), whereas a distance gradient is observable from active snails via hibernation beginning to hibernating snails on the NMDS plot (A versus Hb versus H, Kruskal-Wallis test,  $H = 7.26$ ,  $DF = 2$ ,  $N = 9$ ,  $P = 0.027$ ). Moreover, in terms of bacterial rDNA band number (Figs. 2, 6), the distal intestine seemed to be rich in different bacteria species in active and hibernating snails as well as in snails at hibernation beginning (12, 10 and 6 bands, respectively) compared to the proximal intestine (5, 8 and 4 bands, respectively) and the digestive gland (4, 5 and 3 bands, respectively). In contrast, the non-hibernating snails had a richer bacterial community in the proximal intestine (8 bands), compared to the distal intestine (5 bands) and the digestive gland (6 bands). In terms of abundance of analysed phylotypes (Fig. 8), unclassified bacteria were



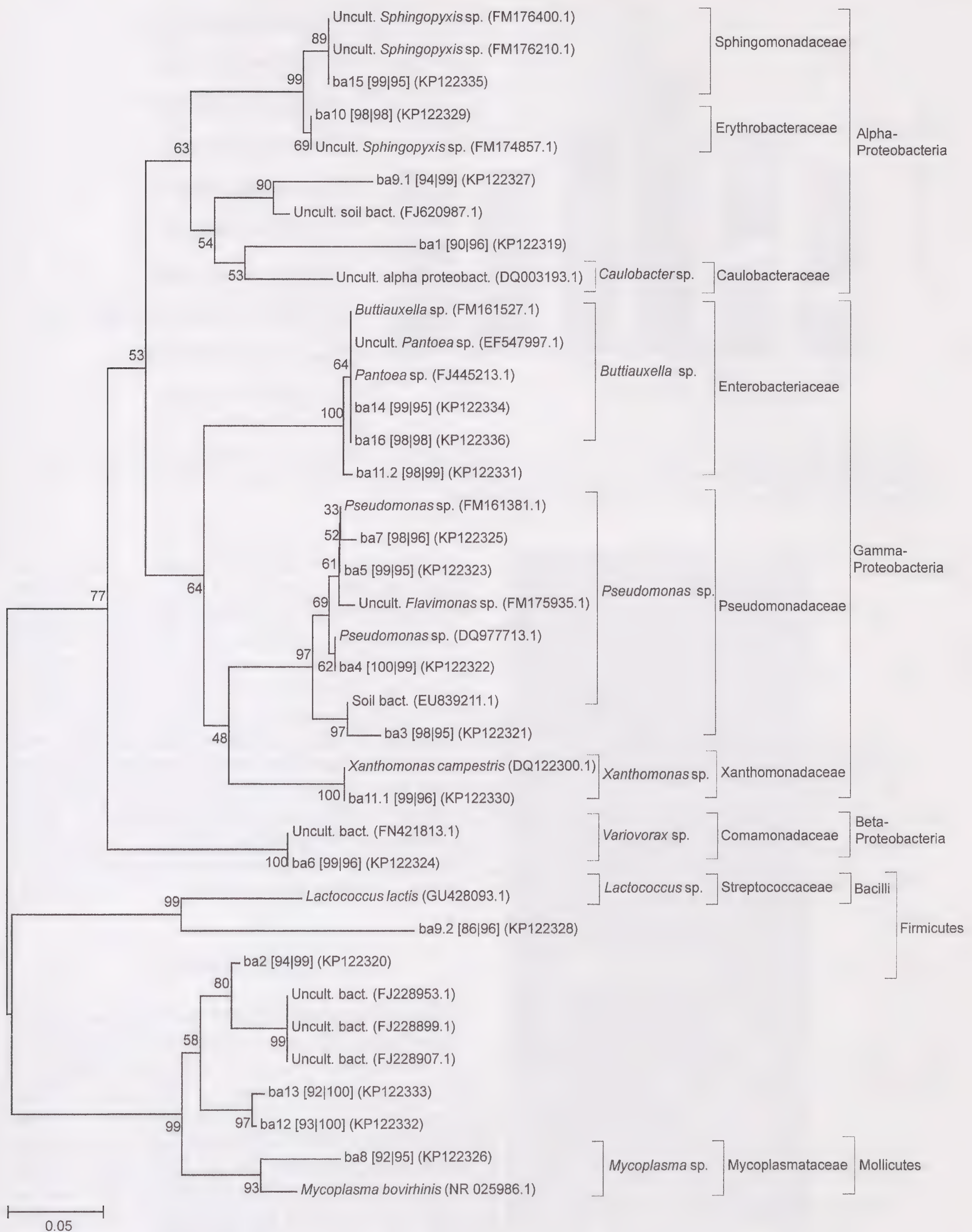


FIG. 4. Neighbour joining tree of 16S rDNA gene sequences ( $N = 18$ ) extracted from gut of *Helix pomatia* depicting the phylogenetic relationships of DGGE band sequences (ba1 – ba16, see Fig. 2) with closest related sequences from the GenBank. The scale bar represents 5% divergence, and bootstrap values (in %) from 1,000 resamplings are shown at the nodes. Values in brackets, following sequences from this study, give the percentage of similarity and query coverage to the closest related sequence derived from GenBank database. All sequences are followed by their accession number from the GenBank database. Taxonomic hierarchy was determined with the RDP classifier tool.



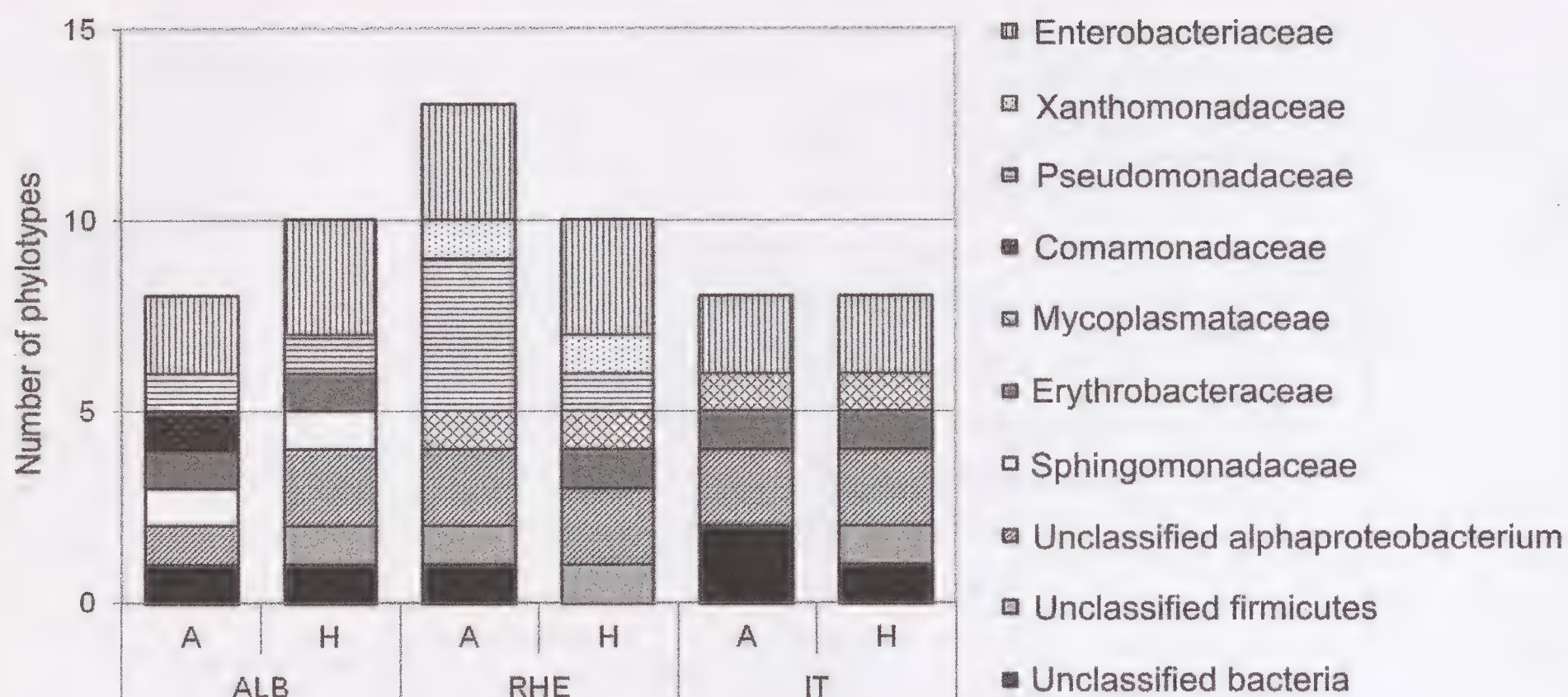


FIG. 5. Number of bacterial phytotypes at the class level in the gut of *Helix pomatia* from three populations (Schwäbische Alb in Germany: ALB, Rhein valley in Germany: RHE, and Italy: IT). Active (A) and hibernating (H) snails were examined.

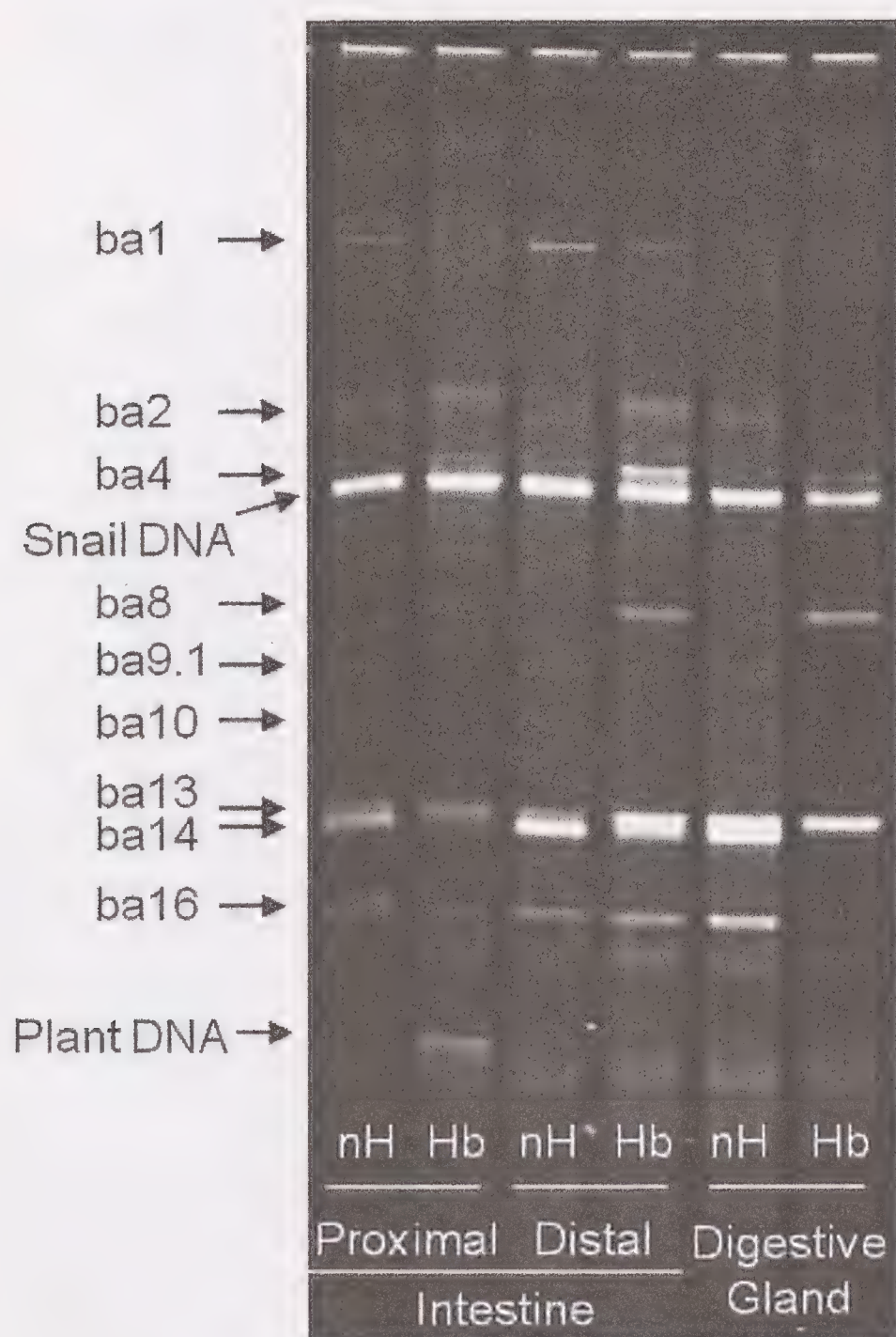


FIG. 6. Fingerprints of the bacterial community in different gut compartment in two physiological states (hibernation beginning: Hb, non hibernating individuals: nH) of the RHE population (Rhein valley in Germany) of *Helix pomatia*. Two bands were sequenced in those lines of 16S rDNA bands, which are indicated by ba1 to ba16. Several bands revealed to be not of bacterial nature after alignment in GenBank (snail and plant DNA).

restricted to the digestive gland in activity, but became abundant in all gut compartments within non hibernating snails as well as in snails at hibernation beginning. Firmicutes, usually present in proximal and distal intestine in both samples, hibernation and hibernation beginning, were present in proximal intestine and digestive gland in non-hibernating snails as well as in distal intestine of active snails. Mollicutes were abundant in all three gut compartments in active snails, but were restricted to distal intestine and digestive gland at hibernation beginning before colonising again the proximal intestine during hibernation.

## DISCUSSION

Functional studies described extensively the importance of bacterial gut flora for the snail's digestion and nutrient providing (Myers & Northcote, 1959; Strasine & Whitaker, 1963; Charrier, 1990). Snails might foster organic matter degradation by bacteria in the intestine where endogenous enzymatic activity is low (Charrier & Rouland, 1992; Flari & Charrier, 1992; Cardoso et al., 2012a). The digestive tract harbours bacteria with metal chelating (Simkiss, 1985) and fermentative activity (Charrier et al., 1998, 2006), particularly on chitin and soluble cellulose, thereby providing nitrogen, lactate and acetate used as precursors and energy sources (Jeuniaux, 1955; Speiser, 2001; Charrier et al., 2006).

The DGGE fingerprinting technique with the NMDS analysis revealed that the intestine of the



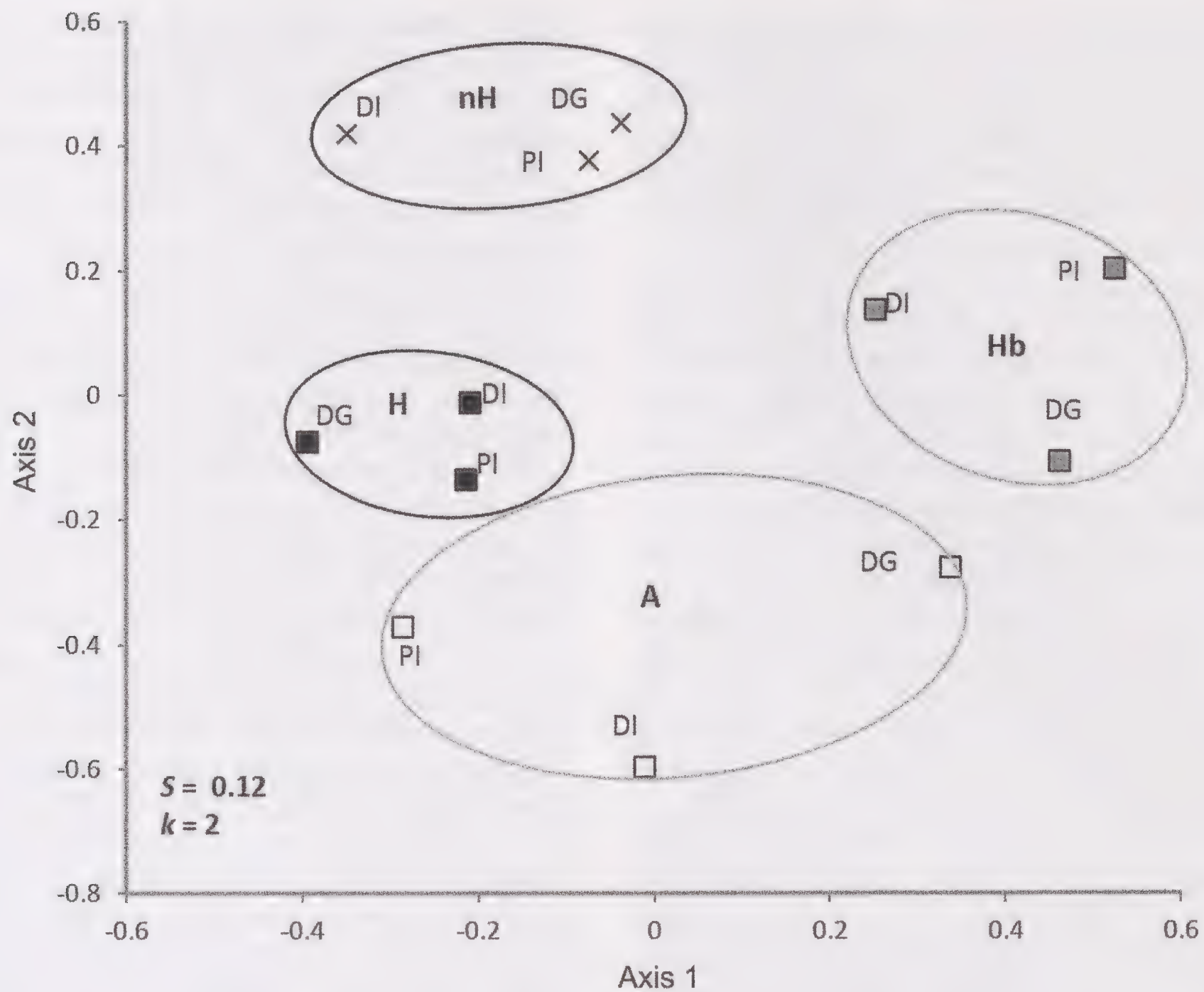


FIG. 7. NMDS plot of bacterial DGGE fingerprinting patterns in the RHE population (Rhein valley in Germany) in different physiological states (activity – A: open symbols, hibernation beginning – Hb: grey symbols, hibernation – H: black symbols, non hibernating individuals – nH: crosses) based on extracted 16S rDNA from the content of different compartments of the digestive tract (proximal intestine: PI, distal intestine: DI, digestive gland: DG) in the land snail *Helix pomatia*.  $S$  indicates the stress and  $k$  the total number of axes used in the analysis. Kruskal-Wallis test of scores between samples on the 1<sup>st</sup> axis:  $H = 6.90$ ,  $DF = 3$ ,  $N = 12$ ,  $P = 0.075$ , and on the 2<sup>nd</sup> axis:  $H = 9.67$ ,  $DF = 3$ ,  $N = 12$ ,  $P = 0.022$ .

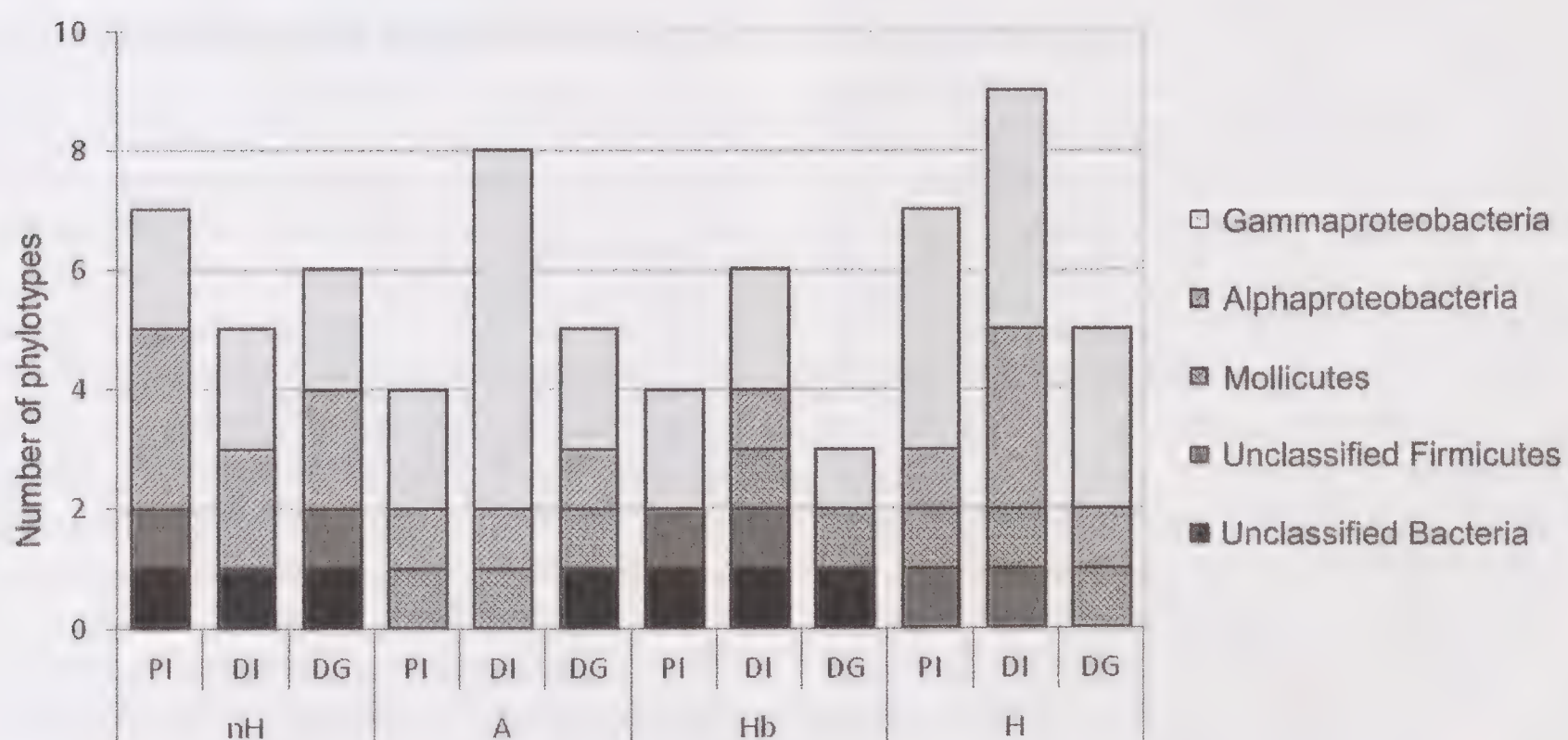


FIG. 8. Number of bacterial phytotypes at the class level per gut compartment (PI – proximal intestine, DI – distal intestine, DG – digestive gland) of *Helix pomatia* from the RHE population (Rhein valley in Germany). Active snails (A), snails at hibernating beginning (Hb) and non-hibernating snails were examined.



land snail *Helix pomatia* harboured a rich bacterial flora specific to each population when snails are in activity. Among the most abundant rDNA fragments, we sequenced Pseudomonadaceae sp. and Enterobacteriaceae that dominated the intestinal and digestive gland community of all populations. According to the work of Kiebre-Toe et al. (2003) and Charrier et al. (2006), *Pseudomonas* sp., *Pantoea* sp. and *Buttiauxella* sp. were the most common strains in the snail's intestine. However, Pseudomonadaceae were absent in the IT population and rare in ALB population. Besides these Gammaproteobacteria, Alphaproteobacteria were abundant. While Sphingomonadaceae were only found in ALB snails, Erythrobacteraceae were present in all populations. From alignment with sequences in GenBank, we could deduce that all these strains come from the environment (Boyd et al., 2007; Austin et al., 2009; Delmotte et al., 2009) and could be ingested with food or by soil scraping according to earlier studies (Charrier, 1990; Watkins & Simkiss, 1990). One strain of unclassified Firmicutes (ba2) appeared among dominant bacteria only in hibernation of all populations, whose closest relatives were sequences obtained from gut content of planorbisid snails (unpublished, Accession numbers FJ228953, FJ228899, FJ228907). Charrier et al. (2006) postulated that bacterial strains isolated from snails in a starved state, like aestivation or hibernation, correspond to eurythermic strains which could be reasonably considered as autochthonous of the snail gut.

The digestive tract of *Helix pomatia* is anatomically as well as physico-chemically compartmentalized (Charrier & Brune, 2003), which was also reflected by the bacterial community structure in this study. The passage of the gut content through the intestinal tract could transiently lead to an enrichment of minor allochthonous bacteria populations in one compartment when it provides favourable environmental conditions (Schmitt-Wagner et al., 2003). This was visible in the proximal intestine and digestive gland in activity of the RHE population.

Because of the exogenous origin of the major community members, micro-environmental conditions like the soil composition, the vegetal food source and climatic factors could influence the bacterial community structure of each snail population. In the land snail *Achatina fulica*, bacterial gut community was modified by diet changes (Cardoso et al. 2012b). Bacteria have different ways to respond to environmental constraints resulting in geographical distribu-

tion patterns that could be reflected by the snail gut colonisation (Balows et al., 2005; Foucaud-Scheunemann & Poquet, 2003). For instance, the Betaproteobacterium present in ALB populations was identified as *Variovorax* sp. previously found in an environmental soil sample of Switzerland (Delmotte et al., 2009). *Variovorax* sp. is an ubiquitous aerobic soil bacterium frequently associated with important biodegradation processes. The organic matter content in the sandy clay soil with pH 5.8 of the ALB habitat leveled 14.63%, whereas only 4.85% were recorded in the sandy loam soil with pH 7.2 in the RHE habitat (Nicolai, 2010). Such soil difference influences the biodegradation activity (Lavelle & Spain, 2005) and might be related to the abundance of *Variovorax* sp. in the snail habitat. Mollicutes, another example, are facultative anaerobes and inhabit plant or mucous animal surfaces (Hayflick & Chanock, 1965). *Mycoplasma* sp. needs cholesterol for growth (Hayflick & Chanock, 1965), which is synthesized *de novo* in land snails (Addink & Ververgaert, 1963; Nicolai et al., 2012b) and which occurs at high level in body fluids of *Helix pomatia* under warm climate conditions (Nicolai et al., 2011). This might explain why mollicutes were only present in RHE and IT populations living in regions of warmer climate.

The differences in the bacterial community structure between snails in activity and snails in hibernation were striking on the NMDS plot. Whereas the snail populations in activity harboured well-discriminated bacterial communities, the snails in hibernation showed approaching community structures. At hibernation beginning, snails expulse the gut content thereby eliminating some phylotypes, such as Mollicutes and Alphaproteobacteria, from the proximal intestine and the later also from the digestive gland. At this moment, unclassified bacteria became abundant in the proximal and distal intestine, but were reduced during hibernation. Gut clearance and physico-chemical changes attended by the initiation of hibernation might induce the restructuration of the bacterial community. Some strains could disappear or being reduced, while other not dominant strains during activity, gain in space and become important during hibernation.

Besides digestive functions, the seasonal dynamic and spatial distribution of bacterial gut community is likely to influence cold hardiness in terrestrial gastropods. Gut bacteria might present ice nucleating activity reducing cold hardiness in partial freezing tolerant snail species like *Helix pomatia* (Nicolai et al., 2005) and



*Cornu aspersum* (Ansart et al., 2002, 2010). *Helix pomatia* decreases slightly its supercooling point from  $-2^{\circ}\text{C}$  in activity to  $-4^{\circ}\text{C}$  –  $-7^{\circ}\text{C}$  in hibernation depending on geographic origin (Nicolai et al., 2005, 2012a). The tested bacteria in the study of Nicolai et al. (2005) and Ansart et al. (2010) revealed a weak ice nucleating activity in the given culture conditions of one bacterial strain persisting during hibernation. By contrast, gut clearance at the initiation of hibernation contribute to a great supercooling ability in freezing intolerant insect species (e.g., Cannon & Block, 1988; Zachariassen, 1980) and could also explain the low freezing temperature ( $-16^{\circ}\text{C}$ ) in the land snail *Anguispira alternata* (Riddle, 1981). Further studies are still necessary to identify ice nucleating active bacteria in the digestive system of land snails.

During hibernation, a bacteria colonised nearly equally all compartments of the intestinal tract. Nourished by mucus secretion (Jeuniaux, 1955; Pereira & Breckenridge, 1981) they maintain the digestive activity, for example, carbohydrase activity (Charrier, 1990; Flari & Charrier, 1992). However, some bacteria can have a role in winter mortality through mitigating cold hardness. In insects, some intestinal bacteria strains attracted much attention in studies about freezing resistance. For example, *Enterobacter agglomerans* and *Enterobacter taylorae* were found in insect guts during activity, initiating ice formation in the insect's body between 0 and  $-5^{\circ}\text{C}$  (Lee et al., 1991). Before winter these strains were actively expelled from the gut, thereby enhancing the supercooling ability of the insect. These ice-nucleating bacteria owe the capacity of freezing initiation at temperatures between  $-10$  and  $0^{\circ}\text{C}$  to the presence of specific proteins on their cell surfaces, as proved in *Pseudomonas fluorescens* (Pseudomonadaceae; Corotto et al., 1986) and *Erwinia herbicola* (Enterobacteriaceae; Warren & Corotto, 1989). *Pseudomonas syringae* was identified as INA responsible for freeze injuries in plants (Lindow et al., 1982), and *Xanthomonas campestris* showed also INA activity (Kim et al., 1987). In earlier studies on freezing resistance in *Helix pomatia* and *Cornu aspersum*, the intestinal content showed ice nucleating activity, which could be inhibited by antibiotics (Ansart et al., 2002) and heat (Ansart et al., 2010). *Kluyvera* sp was identified acting around  $-9^{\circ}\text{C}$ , but persisted in snail gut during hibernation (Nicolai et al., 2005). The possible presence of *Pseudomonas* sp. and specifically *Xanthomonas campestris*, exhibiting an ice-nucleating activity ranging between  $-2^{\circ}\text{C}$  and

$-8^{\circ}\text{C}$  (Kim et al., 1987), in the ALB and RHE snail guts in activity as well as in hibernation is consistent with the supercooling ability in activity of  $-2^{\circ}\text{C}$  and in hibernation of  $-6.7^{\circ}\text{C}$  and  $-5.7^{\circ}\text{C}$  in the ALB and the RHE population, respectively (Nicolai et al., 2012a).

Non-hibernating snails (without epiphragm) were reported in natural conditions. Generally, snails staying without epiphragm do not survive winter (Nietzke, 1970; Kiliass, 1985). Their supercooling activity is low ( $-2.5^{\circ}\text{C}$ ) with some striking increases of metabolites involved in energy producing pathways (succinate, triglycerides) compared to those with epiphragm at hibernation beginning ( $-6.1^{\circ}\text{C}$ , Nicolai et al., 2011). Their community structure within the intestinal tract was close to that in hibernating snails on the NMDS plot, but the diversity of phylotypes resembles to the community of snails at hibernation beginning. Specifically the complete loss of Mollicutes from the whole intestinal tract in non-hibernating snails was striking. However, it remains unclear (i) if the bacterial community reflects poor body conditions, (ii) if pathogen strains were present, or (iii) if the absence of some strains could greatly perturb physiological processes of hibernation initiation. From birds and mammals, it is known that important variations in the intestinal microbial community could have long-term effects on growth, digestion, and immunity (Kohl, 2012).

Despite the method of PCR-DGGE was shown to be adequate to detect and compare differences in microbial community structures (Okubo & Sugiyama, 2009), we could not find the same diversity described by Charrier et al. (2006). DGGE is limited by the fact that profiles show only the most dominant phylotypes in the investigated samples (Claesson et al., 2009), and by pooling samples inter-individual variability in phylotype diversity was lost. Furthermore, some bands from different positions in one column of the DGGE gel were shown to contain the same sequence, for example, ba14 and ba11.2 were assigned to *Pantoea* sp. and ba2, ba12, ba13 were assigned to the same sequences of uncultured bacteria isolated from the gut of planorbid snails. Bacteria can feature up to 15 operons, with less than 1% nucleotide difference, in their genome (Acinas et al., 2004). These small divergences are enough to lead to multiple bands on the DGGE. Such sequence variations could also be introduced artificially as a consequence of PCR amplification (Speksnijder et al., 2001). Another critical issue is the specificity of the primer used which could reduce considerably the number of revealed



bacteria phylotypes, as observed earlier for some other primer sets (Malin & Illmer, 2008). Furthermore, snail and plant DNA appeared on the DGGE gel which shows that some untar-geted amplifications could happen.

In conclusion, *Helix pomatia* harbours permanently a rich gut microbial community, and many transient bacteria colonise the gut only in foraging snails. Therefore, the bacterial community structure might depend on climatic, trophic and soil conditions in the snail habitat. Seasonal dynamic of the bacterial community affects differently all gut compartments and could have an impact on physiological processes linked to cold hardiness. Since the bacterial gut community seems to be vital for the maintenance of organism functioning, specifically during hibernation, the preservation of specific habitat conditions that could have an influence on the bacteria gut community appears crucial for the conservation of this endangered snail species. Agricultural practices, pollution and microclimatic changes alter the community of microorganisms in the soil (Lazzaro et al., 2006) which might have a yet underestimated effect on many ectothermic species that rely on a rich, but seasonally renewable microbial gut community. Therefore, further studies should focus on the individual variation in bacterial community and investigate how it is affected by environmental changes.

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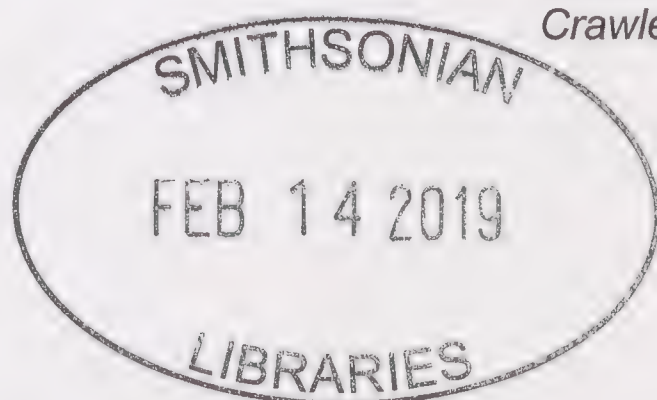
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## ANNOUNCEMENT

The J Frances Allen Institute of Malacology  
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The Board of Directors of the Institute of Malacology, publisher of the academic journal *Malacologia*, is pleased to announce the creation of the J Frances Allen Institute of Malacology Outstanding Publication Award. This cash award of \$500 will be presented for an outstanding paper published in *Malacologia* by a student, with the timing dependent on the superior quality of the student paper as judged by a committee of the IM Board. There is no formal application or deadline. A student submitting a manuscript must be sole or senior author of the paper, and should indicate that the paper being submitted stems from Master's or Ph.D. research to confirm his or her eligibility for the award. The Allen Publication Award was established in 2011 to honor J Frances "Jady" Allen, who provided indispensable help and guidance in establishing the journal *Malacologia*, first published in 1962.



## THE IMPACT OF THREE HERBICIDES ON BIOLOGICAL AND HISTOLOGICAL ASPECTS OF *BIOMPHALARIA ALEXANDRINA*, INTERMEDIATE HOST OF *SCHISTOSOMA MANSONI*

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### ABSTRACT

Schistosomiasis remains a public health problem in the developing world. *Biomphalaria alexandrina* is the intermediate host of *Schistosoma mansoni*, with a widespread distribution in Egypt. In Egypt molluscicides have been important, but otherwise molluscicides have been of minor significance. They may, however, become important now that WHO talks about eradicating schistosomiasis in some countries and that WHO has finally accepted that snail control is important. The present study investigated the different effects of three commercial herbicidal compounds, Butralin (as Amex 48% EC), glyphosate isopropylammonium (Herphosate 48% SL) and Pendimethalin (Stomp 50% EC) on *B. alexandrina*. All three compounds were found to have a molluscicidal effect, with Pendimethalin the most toxic over the examined range of concentrations. In addition, at sublethal concentrations, these compounds reduced growth rates and reproductive output (numbers of eggs laid) in exposed *B. alexandrina*, and it reduced viability of those eggs. Interpretation of assay data was supported by histological changes in the digestive and hermaphrodite glands of snails exposed at a range of concentrations. Moreover, the three compounds were also shown to rapidly (with three hours exposure) induce a toxic effect in miracidiae and cercariae of *Schistosoma mansoni*. It can be concluded that the three herbicidal compounds have molluscicidal and antihelminth properties.

Key words: *Biomphalaria alexandrina*, *Schistosoma mansoni*, miracidiae, cercariae, Butralin, glyphosate isopropylammonium, Pendimethalin, herbicides, molluscicidal activity, antihelminth activity, schistosomiasis.

### INTRODUCTION

Schistosomiasis is a group of chronic parasitic diseases affecting at least 240 million people in more than 70 countries (Larson et al., 2014). In virtually no region on the African continent are people safe from infections by *Schistosoma* species, the causative agents. About 85% of the infected populations worldwide are Africans (WHO, 2010, 2014). The freshwater snail *Biomphalaria alexandrina* (Ehrenberg, 1831) (Mollusca, Planorbidae) is the intermediate host of *Schistosoma mansoni* Sambon, 1907 (Bakry et al., 2011).

Controlling of these snails is still one of the most promising means in the battle against schistosomiasis (Bakry et al., 2012; Mahmoud et al., 2011; Mohamed et al., 2012; WHO, 2014). Some herbicidal compounds may have molluscicidal action, with effects at the

cellular, physiological and molecular levels (Bakry et al., 2015).

In Egypt, various herbicidal compounds are still under investigation. Bakry et al. (2012), for example, found that atrazine and glyphosate to possess a molluscicidal activity on *B. alexandrina*. The current work aims to study the effect of three compounds commonly formulated as herbicides and widely used in Egypt on the biological and histological parameters of *B. alexandrina*.

### MATERIALS AND METHODS

#### Snails

*Biomphalaria alexandrina* snails were collected from freshwater canals in Abu-Rawash (30 km from Cairo), Giza, and maintained at

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the Malacology Laboratory, Theodor Bilharz Research Institute (TBRI), where, they were washed thoroughly with dechlorinated tap water, and maintained in plastic aquaria (16 x 23 x 9 cm). The aquaria were provided with dechlorinated aerated tap water (10 snails/L) and covered with glass plates. They were maintained in an air conditioned room at 24°C, and fluorescent light was reflected 30 cm over them during daytime. Oven-dried lettuce leaves and blue green algae (*Nostoc muscorum*) were used for feeding. Lettuce leaves were given daily, with the amount adjusted to the number and size of the snails. The algae was added weekly. *Nostoc muscorum* algae was originally obtained from Schistosoma Biological Supply Center (SBSC) at Theodor Bilharz Research Institute (TBRI), Imbaba, Giza, Egypt, and were cultivated in Medical Malacology Laboratory, according to Liang et al. (1987). Water in the aquaria was changed weekly. Snails were examined twice weekly for natural trematode infection for one month before being used in bioassay tests.

For collecting egg masses, small pieces of polyethylene sheets were introduced into the aquaria (Pellegrino & Gonçalves, 1965) and harvested daily to obtain eggs of known age.

#### Ova and Cercariae

*Schistosoma mansoni* ova and cercariae were obtained from SBSC, where ova were taken from previously infected mice and cercariae from infected snails. The ova were allowed to hatch in small amount of dechlorinated water (24°C) for about 15 min under a direct light. After hatching of ova, the liberated miracidia were used in the experimental tests.

#### Synthetic Herbicides

Three herbicidal compounds were used in this study: Butralin (formulated as Amex 48% EC; Registration No. 245), glyphosate isopropylammonium (Herphosate 48% SL; Registration No. 733) and Pendimethalin (Stomp 50% EC; Registration No. 200). Commercial formulations were purchased in Egypt from Neopharm, The National Company for Fertilizers & Chemicals (AGROCHEM), and BASF, respectively.

#### Bioassay Tests

##### *Molluscicidal Activity*

Serial dilutions were prepared from Butralin, glyphosate isopropylammonium and Pendimethalin to determine the sublethal concentration. A stock solution of 1,000 ppm was prepared from each compound on the basis of W/V using dechlorinated tap water (pH 7.0–7.5), from which a series of concentrations were prepared for various assays, again in dechlorinated tap water.

In the first assay, a range of concentrations was used to establish the lethal dose in exposed adult snails. Three replicates were used, each of ten snails (6–8 mm shell width), for each concentration. Snails were washed thoroughly with dechlorinated tap water, maintained in plastic aquaria (16 x 23 x 9 cm). The aquaria were provided with dechlorinated aerated tap water (10 snails/L) and covered with glass plates. Exposure and recovery periods were each 24 h (at 25 ± 1°C). For each test, three replicates of control snails were maintained under the same experimental conditions in dechlorinated tap water (WHO, 1965).

The second assay examined the effects of sublethal concentrations on mortality and growth rates of *B. alexandrina*. Snails were exposed to sublethal concentrations (LC<sub>0</sub>, LC<sub>10</sub>, and LC<sub>25</sub> at 24 h) of each herbicidal compound and numbers alive recorded weekly, and their shell width measured with calipers. Both juvenile snails (< 3.6 mm shell width) and adult snails (6–8 mm shell width) (El-Nahas & El-Deeb, 2007), were exposed with three replicates each of ten snails/L. As in the first experiment, also, three replicates of control groups was maintained in clean water.

In the third experiment, the effects of sublethal concentrations on egg-laying capacity were examined. Snails (6–8 mm shell width) were exposed for eight weeks to the concentrations LC<sub>0</sub>, LC<sub>10</sub> and LC<sub>25</sub> of each herbicidal compound for 24 h/week for four successive weeks. Three replicates, each of ten snails/L, were prepared for each concentration, another three replicates for control groups were maintained in dechlorinated water. The following parameters were recorded weekly: mortality rate Lx (proportion of the corrected for mortality among control snails), fecundity Mx (number of eggs/snail/week) and R0 (reproductive rate, as the accumulated product of LxMx) (El-Gindy & Radhawy, 1965).



Lastly, effects of concentrations lethal to adult snails were examined for effects on the viability of snail eggs. For each concentration ( $LC_0$ ,  $LC_{10}$ , and  $LC_{25}$ ,  $LC_{50}$  and  $LC_{90}$ ), three replicates comprising about 50 eggs/100 ml) of 1, 3 and 7 days old were prepared and exposed for 24 h, then transferred to clean water to calculate the rate of hatching of eggs in each concentration. Hatchability was calculated by dividing the number of newly hatched snails by the total number of eggs at the beginning of the experiment. Other three groups of eggs (1, 3 and 7 days old) were maintained in clean dechlorinated water ( $25 \pm 1^\circ C$ ) as control groups.

#### Miracidicidal and Cercaricidal Activity

The three compounds in a range of concentrations that had been tested against adult snails ( $LC_0$ ,  $LC_{10}$ , and  $LC_{25}$ ,  $LC_{50}$  and  $LC_{90}$ ) were examined for their effects on *S. mansoni* miracidiae and cercariae. Five ml of water containing about 100 fresh hatched miracidiae was pipetted into a cell in a divided Petri dish, and five ml water containing 100 freshly shed *S. mansoni* cercariae pipetted in another, and to each five ml of double-strength concentration added from each compound. Another, three groups of 10 ml dechlorinated tap water containing 100 freshly shed cercariae per each group was kept as controls (Ritchie et al., 1974). Mortality after intervals of 15, 30, 45, 60, 120, 180, 240, 300 and 360 min was recorded. Observations on the movement and mortality of miracidiae and cercariae were recorded at different intervals of exposure under a dissecting microscope. Stationary miracidia and cercariae were assumed to be dead, cercariae with their heads separated from tails were considered dead, and mortality in both tested and control groups was recorded. Histological changes in the digestive and hermaphrodite glands of treated adult snails

(8–10 mm in shell diameter) were studied after exposure to  $LC_0$ ,  $LC_{10}$ , and  $LC_{25}$  sublethal concentrations for 24 h/week for two successive weeks and compared with control snails, according to Mohamed & Saad (1990). Thereafter, both treated and control snails were washed with water, and then dried with ethyl alcohol (70%) (five snails from each group). The shells were gently crushed between two glass slides and the soft parts of the snails were carefully removed out of the shell. The hermaphrodite and the digestive glands of each snail were gently separated and fixed in Bouin's solution. The glands were dehydrated using ascending grades of ethanol, cleared in terpinol, embedded in paraffin wax and finally sectioned at 6  $\mu$ . Sections were stained with hematoxyline and eosin stain (H-E), then left to dry. The stained slides were examined and photographed by a germin polarized photomicroscope supplied by Zeiss Video camera.

#### Statistical Analysis

Lethal concentration values were computed for each assay (Litchfield & Wilcoxon, 1949). Comparison of means of experimental and control groups was carried out using Student's t-test (Spiegel, 1981). Values were expressed as mean  $\pm$  S.D., and the obtained data were analyzed using the Graph Pad Prism 6.04 software for Windows (Graph Pad Software, San Diego, California, U.S.A.; 1992–2014).

## RESULTS

#### Molluscicidal Activity

In the present study, it was observed that Pendimethalin was found to be more toxic to *B. alexandrina* snails than Butralin and glyphosate isopropyl ammonium (Table 1). On the basis of

TABLE 1. Molluscicidal activity of the tested herbicidal compounds against adult *Biomphalaria alexandrina* (24 hours exposure);  $LC_x$  = the concentration at which x percent mortality occurred.

| Compound                          | $LC_0$<br>ppm | $LC_{10}$<br>ppm | $LC_{25}$<br>ppm | $LC_{50}$<br>ppm | Confidence<br>limits of<br>$LC_{50}$ PPM | $LC_{90}$<br>ppm | Confidence<br>limits of<br>$LC_{90}$ PPM | Slope of re-<br>gression mor-<br>tality on conc. |
|-----------------------------------|---------------|------------------|------------------|------------------|------------------------------------------|------------------|------------------------------------------|--------------------------------------------------|
| Butralin                          | 0.556         | 2.417            | 3.906            | 5.560            | (3.70–8.34)                              | 8.703            | (6.22–12.80)                             | 1.093                                            |
| Glyphosate iso-<br>propylammonium | 1.506         | 3.875            | 9.174            | 15.062           | (9.13–16.57)                             | 26.249           | (23.87–28.90)                            | 0.335                                            |
| Pendimethalin                     | 0.2148        | 0.535            | 1.299            | 2.148            | (1.43–3.22)                              | 3.762            | (2.40–6.02)                              | 1.820                                            |



TABLE 2. The survival rate and growth rate of juvenile *Biomphalaria alexandrina* snails exposed to sublethal concentrations of three herbicidal compounds for exposure for eight weeks.

|                              |                  | Survival rate (%) |      |      |      |      |      |      |      |      | Growth rate (%) |          |
|------------------------------|------------------|-------------------|------|------|------|------|------|------|------|------|-----------------|----------|
|                              |                  | Weeks             |      |      |      |      |      |      |      |      |                 |          |
| Conc. (ppm)                  |                  | 0                 | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8    | 1st four        | 2nd four |
| Butralin                     | LC <sub>0</sub>  |                   |      |      |      |      |      |      |      |      |                 |          |
|                              | (0.556)          | 100               | 95   | 87   | 81   | 69   | 55   | 22.5 | 15.8 | 8.3* | 19.34           | 31.72**  |
|                              | LC <sub>10</sub> |                   |      |      |      |      |      |      |      |      |                 |          |
|                              | (2.41)           | 100               | 87   | 69   | 45   | 38.5 | 18   | 5.3  |      |      | 18.01           | 13.428   |
|                              | LC <sub>25</sub> |                   |      |      |      |      |      |      |      |      |                 |          |
|                              | (3.906)          | 100               | 80   | 55   | 25   | 8.3  |      |      |      |      | 11.11           |          |
| Glyphosate isopropylammonium | LC <sub>0</sub>  |                   |      |      |      |      |      |      |      |      |                 |          |
|                              | (1.506)          | 100               | 90   | 80   | 71.5 | 48.3 | 38   | 26.5 | 18   | 18   | 19.23           | 33.22    |
|                              | LC <sub>10</sub> |                   |      |      |      |      |      |      |      |      |                 |          |
|                              | (3.87)           | 100               | 70   | 59   | 45   | 25   | 14   | 7.5  |      |      | 17.69           | 9.67     |
|                              | LC <sub>25</sub> |                   |      |      |      |      |      |      |      |      |                 |          |
|                              | (9.17)           | 100               | 66.5 | 41.5 | 21.5 | 6.6  |      |      |      |      | 16.53           |          |
| Pendimethalin                | LC <sub>0</sub>  |                   |      |      |      |      |      |      |      |      |                 |          |
|                              | (0.214)          | 100               | 85   | 80   | 66   | 45   | 36.5 | 18   | 15   | 5    | 24.78           | 14.98    |
|                              | LC <sub>10</sub> |                   |      |      |      |      |      |      |      |      |                 |          |
|                              | (0.535)          | 100               | 80   | 72   | 56.5 | 46.5 | 18   |      |      |      | 12.46           | 2.45     |
|                              | LC <sub>25</sub> |                   |      |      |      |      |      |      |      |      |                 |          |
|                              | (1.299)          | 100               | 56   | 26   | 16.5 | 5    |      |      |      |      | 12.55           |          |
| Control                      |                  | 100               | 98   | 97   | 95   | 95   | 91   | 83   | 75   | 75   | 61.41           | 66.32    |

\* The mean of the percentage survival in the three replicates.  
\*\*The mean of the percentage Growth rate in the three replicates.

LC<sub>50</sub> values, Pendimethalin toxicity to the snails was about 2.58 times that of Butralin and 7.012 times of glyphosate isopropylammonium.

The growth rates of snails exposed to LC<sub>0</sub>, LC<sub>10</sub> and LC<sub>25</sub> of the three compounds over four weeks were highly significantly reduced ( $p < 0.01$ ) compared to the control group (Table 2). Also, survival rates of juvenile snails were reduced after their exposure to the tested concentrations of these herbicides.

The reproductive rate ( $R_0$ ) of snails was significantly reduced when exposed to the herbicidal compounds ( $p < 0.001$ ) (Table 3). Also, survival rate ( $L_x$ ) of adult *B. alexandrina* snails decreased with an increase in the applied concentrations. The high sublethal concentrations (LC<sub>25</sub>) of the three herbicides reduced survival rate of adult snails.

Viability of *B. alexandrina* eggs were affected non significantly by their exposure to the concentrations of Butralin, Pendimethalin and

glyphosate isopropylammonium that did not affect mortality in adult snails (i.e., the LC<sub>0</sub>). However, the hatchability of eggs of age one and three days at the time of exposure to the respective compounds was markedly lower than those of seven day-old eggs at times of exposure (Table 4). At LC<sub>90</sub>, no hatching of eggs occurred when exposed to butralin or pendimethalin, but with those eggs exposed to glyphosate isopropyl ammonium a low. At LC<sub>90</sub>, there is 20% hatchability of eggs at age one day, 2% for seven day-old eggs, while no hatchability at three day-old eggs in snails subject to glyphosate herbicide.

Miracidicidal and Cercaricidal Activity

Mortality rate of miracidiae and cercariae were increased significantly by increasing the concentration of the herbicidal compounds and the length of the exposure period (Tables 5, 6).



TABLE 3. Survival rate and reproductive rate of *Biomphalaria alexandrina* snails exposed to sublethal concentrations of three herbicidal compounds for four weeks followed by four weeks recovery period.

|                              |                  | Survival rate of adult snails |      |      |      |      |      |      |      |       | Reproductive rate (%) |               |
|------------------------------|------------------|-------------------------------|------|------|------|------|------|------|------|-------|-----------------------|---------------|
|                              |                  | Weeks                         |      |      |      |      |      |      |      |       | R <sub>0</sub>        | Reduction (%) |
| Conc. (ppm)                  |                  | 0                             | 1    | 2    | 3    | 4    | 5    | 6    | 7    | 8     |                       |               |
| Butralin                     | LC <sub>0</sub>  |                               |      |      |      |      |      |      |      |       |                       |               |
|                              | (0.556)          | 1.0                           | 0.95 | 0.88 | 0.80 | 0.70 | 0.60 | 0.20 | 0.10 | 0.05# | 7.05***               | 84.05         |
|                              | LC <sub>10</sub> |                               |      |      |      |      |      |      |      |       |                       |               |
| Glyphosate isopropylammonium | (2.41)           | 1.0                           | 0.88 | 0.76 | 0.50 | 0.30 | 0.20 | 0.07 |      |       | 4.52***               | 89.76         |
|                              | LC <sub>25</sub> |                               |      |      |      |      |      |      |      |       |                       |               |
|                              | (3.906)          | 1.0                           | 0.81 | 0.73 | 0.30 | 0.05 |      |      |      |       | 4.04 ***              | 90.84         |
| Pendimethalin                | LC <sub>0</sub>  |                               |      |      |      |      |      |      |      |       |                       |               |
|                              | (1.506)          | 1.0                           | 0.90 | 0.78 | 0.60 | 0.48 | 0.30 | 0.25 | 0.20 | 0.11  | 4.87***               | 88.99         |
|                              | LC <sub>10</sub> |                               |      |      |      |      |      |      |      |       |                       |               |
| Control                      | (3.87)           | 1.0                           | 0.81 | 0.61 | 0.50 | 0.16 | 0.10 | 0.05 |      |       | 4.20***               | 90.48         |
|                              | LC <sub>25</sub> |                               |      |      |      |      |      |      |      |       |                       |               |
|                              | (9.17)           | 1.0                           | 0.72 | 0.55 | 0.20 | 0.11 |      |      |      |       | 4.23***               | 90.42         |
| Control                      | LC <sub>0</sub>  |                               |      |      |      |      |      |      |      |       |                       |               |
|                              | (0.214)          | 1.0                           | 0.86 | 0.82 | 0.65 | 0.50 | 0.36 | 0.18 | 0.11 | 0.05  | 5.18***               | 88.28         |
|                              | LC <sub>10</sub> |                               |      |      |      |      |      |      |      |       |                       |               |
| Control                      | (0.535)          | 1.0                           | 0.83 | 0.76 | 0.72 | 0.35 | 0.14 |      |      |       | 4.75***               | 89.25         |
|                              | LC <sub>25</sub> |                               |      |      |      |      |      |      |      |       |                       |               |
|                              | (1.299)          | 1.0                           | 0.66 | 0.41 | 0.26 | 0.11 |      |      |      |       | 4.27***               | 90.33         |
| Control                      |                  | 1.0                           | 0.99 | 0.98 | 0.95 | 0.91 | 0.90 | 0.85 | 0.85 | 0.08  | 44.231                |               |

# The mean of the percentage survival in the three replicates.  
\*\*\*Differ from control at p < 0.001.

Histopathological changes of the digestive and hermaphrodite glands in adults treated snails (all at x 40) were expressed as follows:

*Digestive Gland*  
The normal digestive gland occupies a considerable part of the visceral hump and

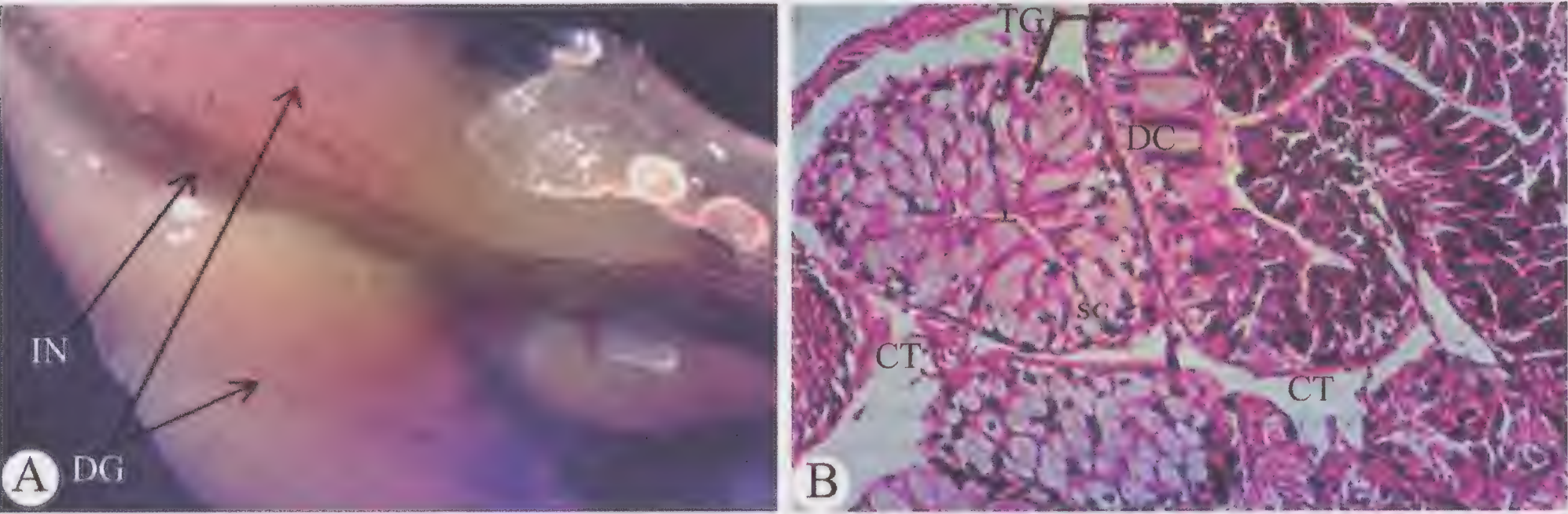


FIG. 1A: Photograph showing a dissection of a control of snails to show lobes of the digestive gland; B: Photomicrograph showing a histological section in the digestive gland of normal *B. alexandrina* snails.



TABLE 4. Effect of three herbicidal compounds (24 hours exposure) on hatchability of *Biomphalaria alexandrina* eggs of 1, 3 and 7 days old at time of exposure.

|                              |                  | % Mean number of hatchability of eggs |                    |                    |
|------------------------------|------------------|---------------------------------------|--------------------|--------------------|
| Conc. (ppm)                  |                  | 1 day at exposure                     | 3 days at exposure | 7 days at exposure |
| Butralin                     | LC <sub>0</sub>  | 92                                    | 95                 | 93                 |
|                              | LC <sub>10</sub> | 82                                    | 32                 | 90                 |
|                              | LC <sub>25</sub> | 24                                    | 18                 | 65                 |
|                              | LC <sub>50</sub> | 6                                     | 4                  | 30                 |
|                              | LC <sub>90</sub> | 0                                     | 0                  | 0                  |
| Glyphosate isopropylammonium | LC <sub>0</sub>  | 89                                    | 88                 | 89                 |
|                              | LC <sub>10</sub> | 58                                    | 22                 | 72                 |
|                              | LC <sub>25</sub> | 46                                    | 12                 | 30                 |
|                              | LC <sub>50</sub> | 32                                    | 2                  | 13                 |
|                              | LC <sub>90</sub> | 20                                    | 0                  | 2                  |
| Pendimethalin                | LC <sub>0</sub>  | 90                                    | 84                 | 94                 |
|                              | LC <sub>10</sub> | 30                                    | 60                 | 74                 |
|                              | LC <sub>25</sub> | 5                                     | 10                 | 27                 |
|                              | LC <sub>50</sub> | 0                                     | 0                  | 8                  |
|                              | LC <sub>90</sub> | 0                                     | 0                  | 0                  |
| Control                      |                  | 99                                    | 98                 | 99                 |

consists of two unequal lobes (Fig. 1A). The normal digestive gland consists of a number of tubular glands; each tubule is lined with one layer with two main histological types of cells; the digestive cells and the secretory cells ( Fig. 1B).

Effect of the Three Herbicides on Digestive Glands

The present study (Fig. 2A) shows moderate pathological damages in the digestive gland after exposure to three herbicides, while, in intensive pathological damage, as most of the connective tissue was broken down so the intertubular space becomes distinctive around the digestive tubules (Fig. 3). The cells lost their identical shape resulting from dissolution of their cell membrane (syncytium), and the lumen inside tubule increased (in the three herbicides). While the most

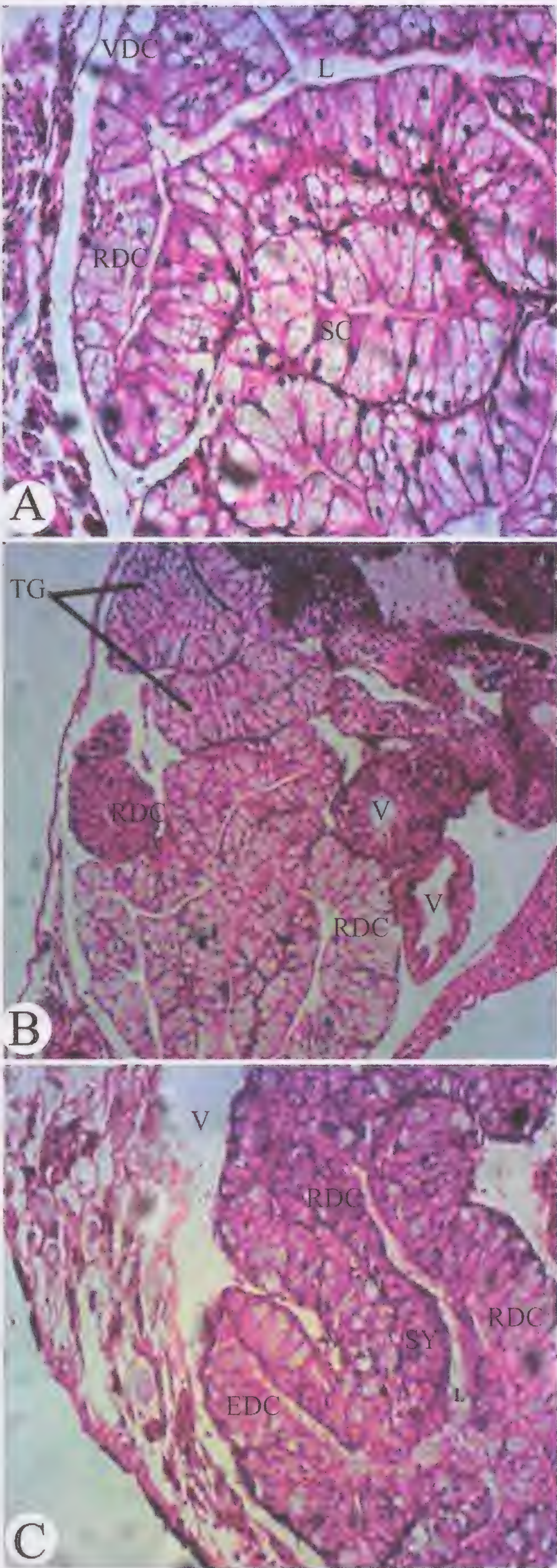


FIG. 2. Photomicrograph showing histological sections through the digestive glands of treated snails with LC<sub>0</sub> sublethal doses for two weeks (H & E). A: Amex 48% EC; B: Herphosate 48% SL; C: Stomp 50% EC.



TABLE 5. Effect of three herbicidal compounds on the mortality rate of *Schistosoma mansoni* miracidia.

| Conc. (ppm)                          |                  | % Mean of mortality |     |     |     |     |     |     |     |
|--------------------------------------|------------------|---------------------|-----|-----|-----|-----|-----|-----|-----|
|                                      |                  | 15                  | 30  | 45  | 60  | 90  | 120 | 150 | 180 |
| Butralin                             | LC <sub>0</sub>  | 0                   | 0   | 2   | 6   | 15  | 30  | 60  | 90  |
|                                      | LC <sub>10</sub> | 0                   | 4   | 10  | 12  | 16  | 29  | 50  | 89  |
|                                      | LC <sub>25</sub> | 12                  | 39  | 52  | 78  | 93  | 100 |     |     |
|                                      | LC <sub>50</sub> | 45                  | 73  | 81  | 100 |     |     |     |     |
|                                      | LC <sub>90</sub> | 60                  | 100 |     |     |     |     |     |     |
| Glyphosate<br>isopropylam-<br>monium | LC <sub>0</sub>  | 0                   | 0   | 14  | 20  | 25  | 40  | 70  | 93  |
|                                      | LC <sub>10</sub> | 15                  | 23  | 31  | 43  | 81  | 100 |     |     |
|                                      | LC <sub>25</sub> | 19                  | 46  | 84  | 100 |     |     |     |     |
|                                      | LC <sub>50</sub> | 42                  | 65  | 100 |     |     |     |     |     |
|                                      | LC <sub>90</sub> | 78                  | 98  | 100 |     |     |     |     |     |
| Pendimethalin                        | LC <sub>0</sub>  | 0                   | 4   | 14  | 23  | 34  | 60  | 71  | 87  |
|                                      | LC <sub>10</sub> | 2                   | 9   | 30  | 55  | 78  | 89  | 96  | 100 |
|                                      | LC <sub>25</sub> | 19                  | 34  | 69  | 82  | 100 |     |     |     |
|                                      | LC <sub>50</sub> | 32                  | 73  | 100 |     |     |     |     |     |
|                                      | LC <sub>90</sub> | 75                  | 100 | 0   |     |     |     |     |     |
| Control                              |                  | 0                   | 0   | 0   | 6   | 12  | 17  | 20  | 50  |

TABLE 6. Effect of three herbicidal compounds on the mortality rate of *Schistosoma man-soni* cercariae.

| Conc. (ppm)                          |                  | % Mean of mortality |     |     |     |     |     |     |     |
|--------------------------------------|------------------|---------------------|-----|-----|-----|-----|-----|-----|-----|
|                                      |                  | 15                  | 30  | 45  | 60  | 90  | 120 | 150 | 180 |
| Butralin                             | LC <sub>0</sub>  | 0                   | 4   | 6   | 9   | 30  | 58  | 70  | 99  |
|                                      | LC <sub>10</sub> | 6                   | 20  | 30  | 60  | 98  | 100 |     |     |
|                                      | LC <sub>25</sub> | 9                   | 30  | 90  | 98  | 100 |     |     |     |
|                                      | LC <sub>50</sub> | 30                  | 66  | 87  | 100 |     |     |     |     |
|                                      | LC <sub>90</sub> | 44                  | 98  | 100 |     |     |     |     |     |
| Glyphosate<br>isopropylam-<br>monium | LC <sub>0</sub>  | 3                   | 10  | 13  | 15  | 30  | 40  | 55  | 89  |
|                                      | LC <sub>10</sub> | 15                  | 50  | 60  | 65  | 85  | 100 |     |     |
|                                      | LC <sub>25</sub> | 20                  | 65  | 70  | 90  | 100 |     |     |     |
|                                      | LC <sub>50</sub> | 75                  | 87  | 91  | 100 |     |     |     |     |
|                                      | LC <sub>90</sub> | 80                  | 98  | 100 |     |     |     |     |     |
| Pendimethalin                        | LC <sub>0</sub>  | 0                   | 3   | 10  | 15  | 60  | 77  | 86  | 99  |
|                                      | LC <sub>10</sub> | 7                   | 16  | 30  | 80  | 95  | 100 |     |     |
|                                      | LC <sub>25</sub> | 15                  | 25  | 53  | 100 |     |     |     |     |
|                                      | LC <sub>50</sub> | 35                  | 76  | 98  | 100 |     |     |     |     |
|                                      | LC <sub>90</sub> | 66                  | 100 |     |     |     |     |     |     |
| Control                              |                  | 0                   | 0   | 3   | 10  | 22  | 45  | 67  | 80  |



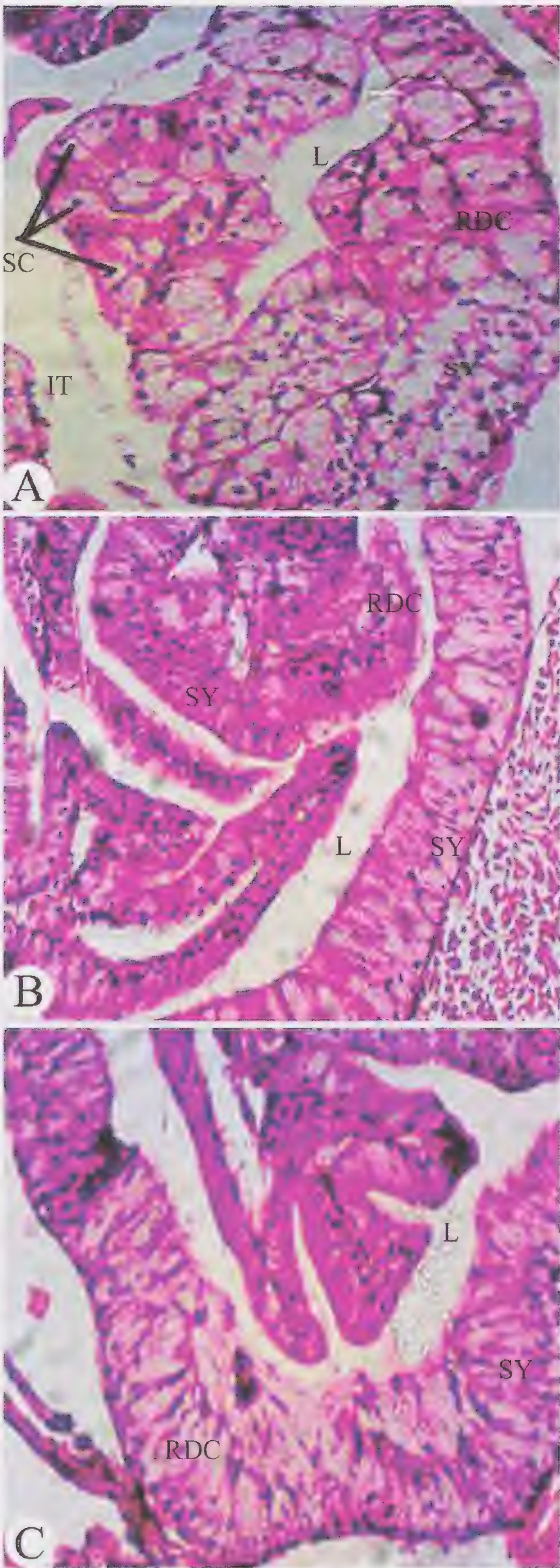


FIG. 3. Photomicrograph showing histological sections through the digestive glands of treated snails with LC<sub>10</sub> sublethal doses for two weeks. A: Amex 48% EC; B: Herphosate 48% SL; C: Stomp 50% EC.

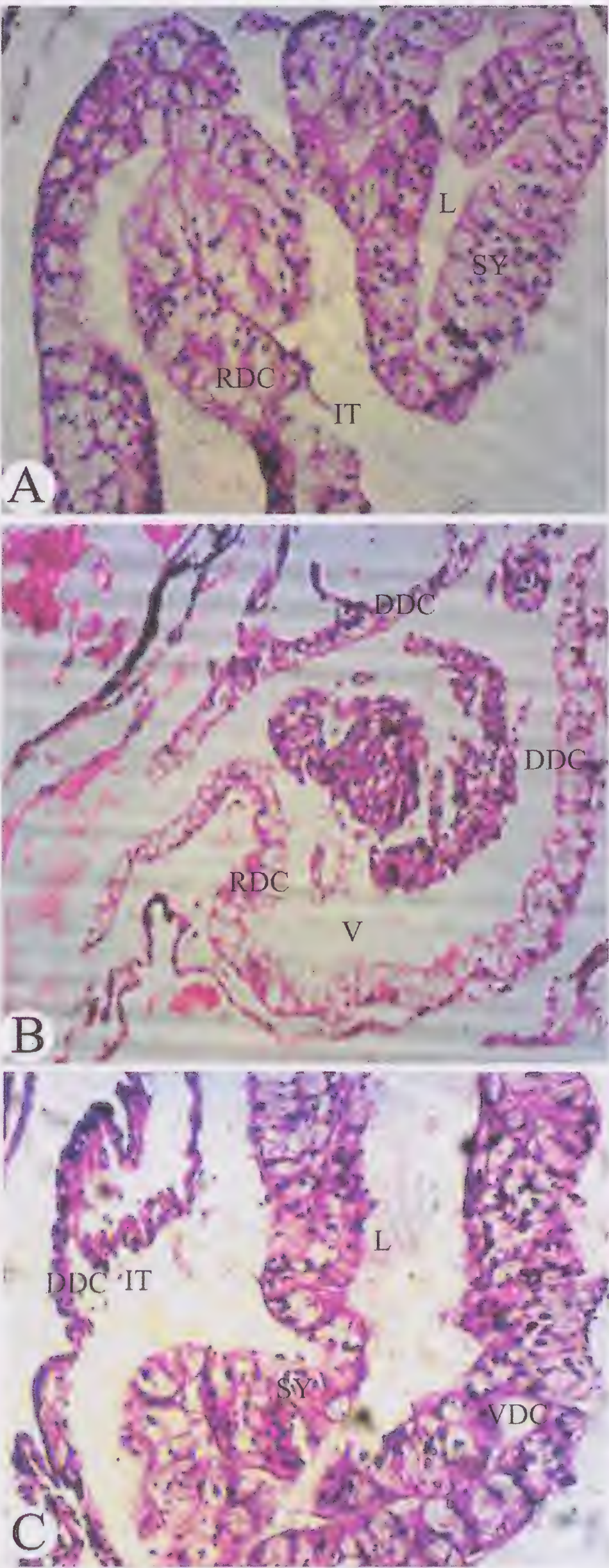


FIG. 4. Photomicrograph showing histological sections through the digestive glands of treated snails with LC<sub>25</sub> sublethal doses for two weeks (H & E). A: Amex 48% EC; B: Herphosate 48% SL; C: Stomp 50% EC. DDG: Degenerated Digestive Cells, DSC: Degenerated Secretory Cells, TG: Tubular Gland, DF: Digested Food, IT: Inter Tubular Space, SC: Secretory Cells, VDC: Vacuolated Digestive Cell, RDC: Ruptured Digestive Cells, V: Vacuole, SY: Syncytium.



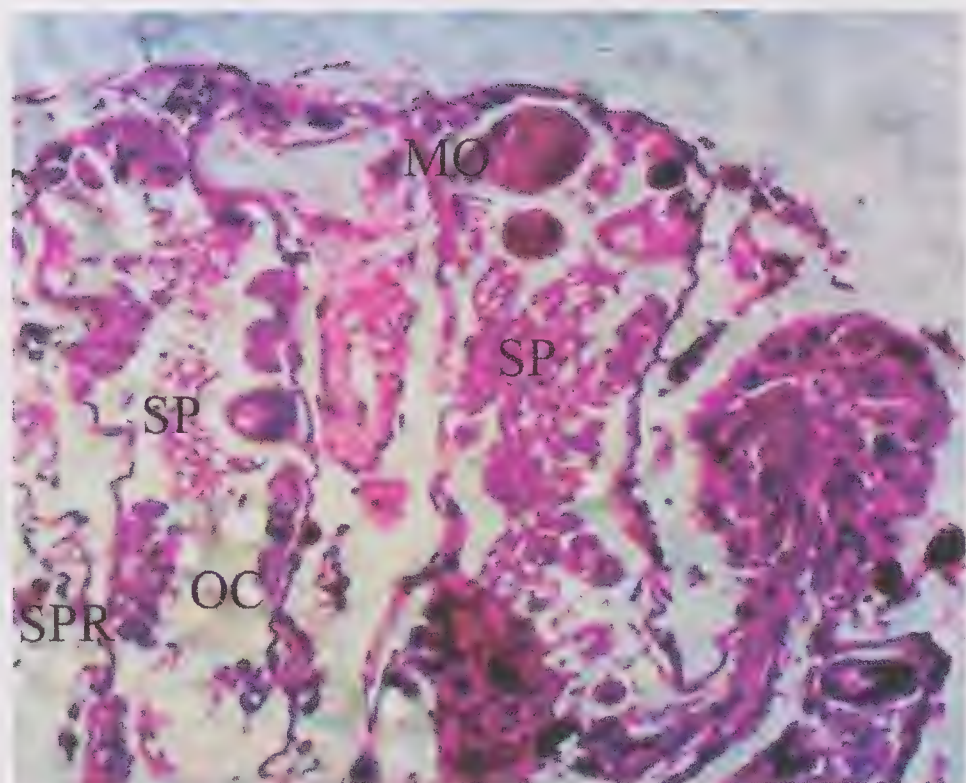


FIG. 5. Photomicrograph showing histological sections through hermaphrodite glands of normal *B. alexandrina* snails (H & E) (x 40). MO: Mature Ova, SP: Sperm, OC: Oocyte, SPR: Spermatocytes.

destructive effect in the digestive tissue was shown with snails subjected to  $LC_{25}$  (Fig. 4), where there is a great loss of identical shape of digestive cells (syncytium).

#### Normal Hermaphrodite Gland of the Adult *B. alexandrina* Snails

The hermaphrodite gland of the normal *B. alexandrina* snails is composed of a number of acini connected together by areolar connective tissue. The male reproductive cells (spermatogonia) are differentiated in clusters forming primary and secondary spermatocytes. The fully developed sperms were observed either in the lumen or attached to sertoli cell, with comparatively small heads and long tails. On the other hand, the female oogenic cells filled the acinar lumen as primary, secondary oocytes and mature ova. The mature ova contain large accumulations of yolk material (Fig. 5).

#### Effect of the Three Herbicides on Hermaphrodite Gland

Treatment of normal *B. alexandrina* snails with Amex at this sublethal dose for two weeks made marked morphological changes

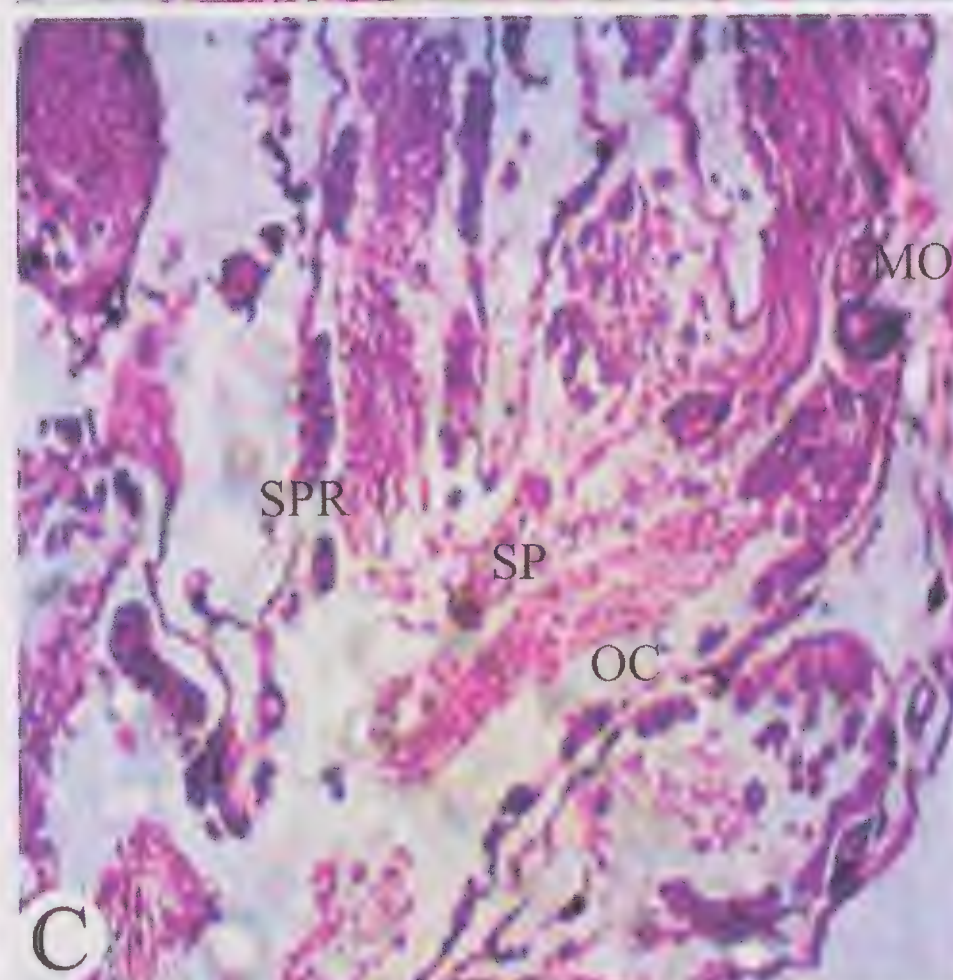
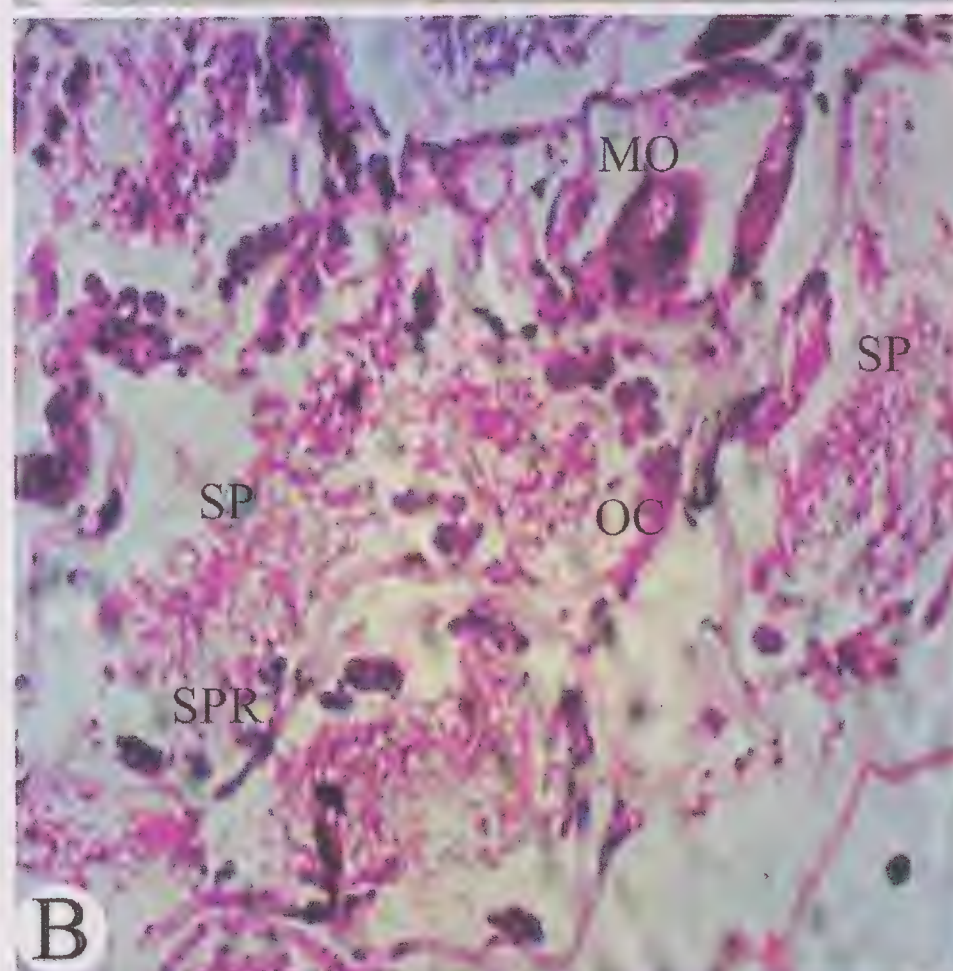
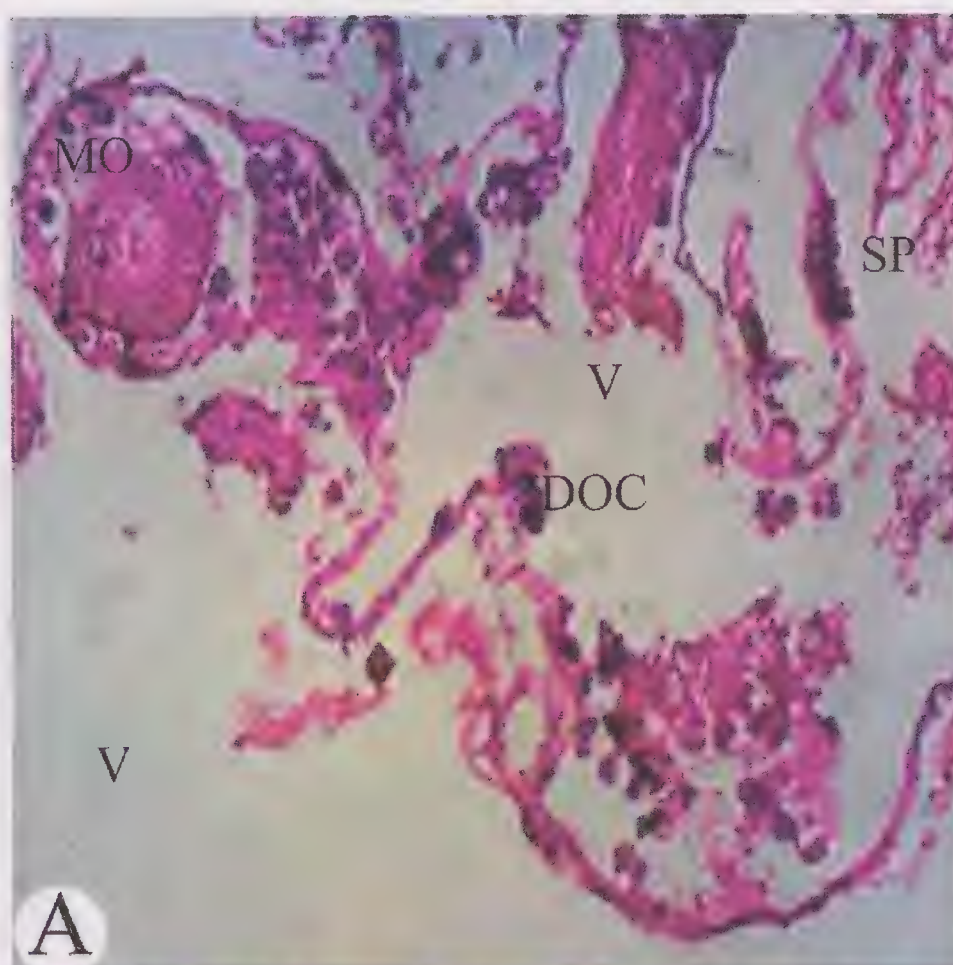


FIG. 6. Photomicrograph showing histological sections through hermaphrodite glands of treated snails with  $LC_0$  sublethal doses for two weeks (H & E). A: Amex 48% EC; B: Herphosate 48% SL; C: Stomp 50% EC.





to gland cells in addition to several evacuations of its tubules from gametogenic stages (Fig. 6). However, they still have mature ovum and few sperm in snails, whereas in snails treated with Herphosate and Stomp, there are increases in sperm. While, as shown in Figure 7, both male and female gonadal cells are highly affected. The greatest damage to gonadal cells occurred by using the three herbicides at  $LC_{25}$  (Fig. 8), where ova lost their shape and degenerated, sperm are reduced and degenerated. Most of the spermatogenic and oogenic stages disappeared.

## DISCUSSION

The present results showed that Pendimethalin (Stomp 50% EC) herbicide was more toxic to *B. alexandrina* snails than the other two herbicides. The differences in the activity of the compounds could be attributed to the differences in their pathways of penetration inside the treated organisms, as well as to the differences in their mode of action on the target organ (Etges & Guilberton, 1966), or they could be attributed to differences in the nature of their active constituents (Hasheesh et al., 2011).

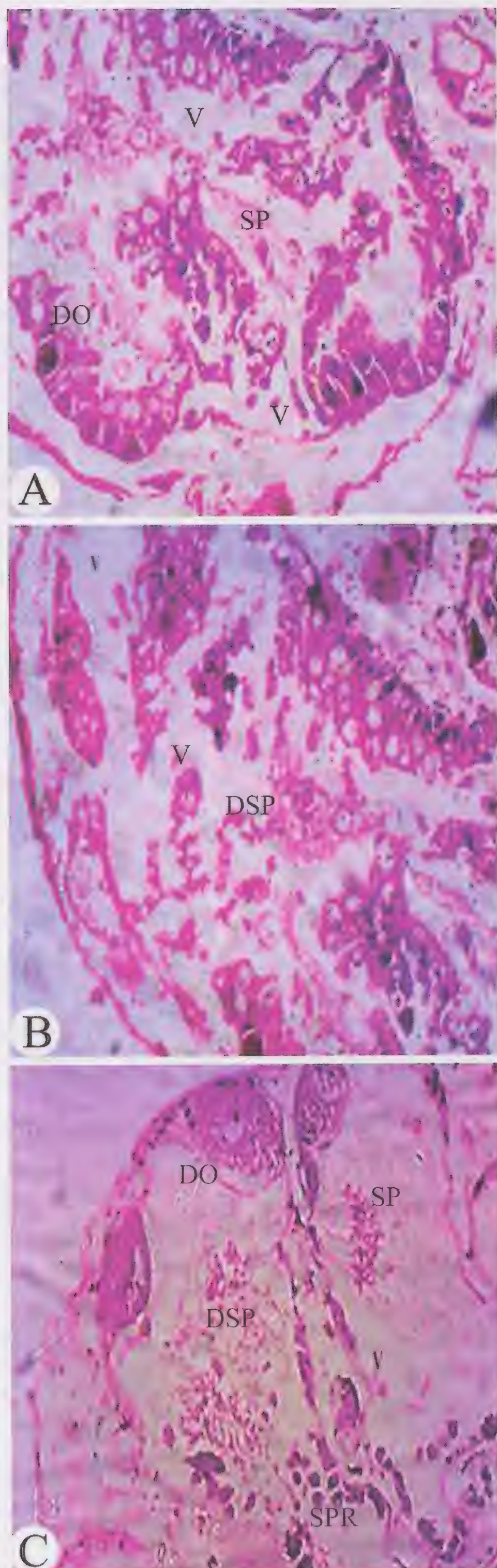
The current data showed that the growth rates of *B. alexandrina* juvenile snails exposed to the tested herbicides were less than that of controls. This may be related to their physiological and biological activities being partially interrupted, or the snails may allocate their energy for maintenance (Mohamed et al., 2012).

The present data showed that, survival rates of juvenile snails were reduced after their exposure to the tested concentrations of these herbicides. It could be that these survived snails tried to overcome the residual toxic effects of the tested agents and their effort to compensate the harmful stress they suffered during the exposure period (Mohamed et al., 2012). When using Pendimethalin, it decreased again, because of the high damage to their digestive system. The same results obtained by Bakry et al. (2012), who showed that  $LC_{10}$  of the two pesticides (Atrazine and Roundup)

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FIG. 7. Photomicrograph showing histological sections through hermaphrodite glands of treated snails with  $LC_{10}$  sublethal doses for two weeks (H & E). A Amex 48% EC; B: Herphosate 48% SL; C: Stomp 50% EC.





caused a considerable reduction in the survival rates and egg production of treated snails. Also, Hasheesh & Mohamed (2011) evaluated the molluscicidal activity of two pesticides (Chlorpyrifos and Profenophos) against *Bulinus truncatus* snails, and they found that these pesticides highly reduced the survival rate, egg production and growth rate of these snails. They confirmed this reduction by histological examinations, which showed severe damage in the digestive and hermaphrodite gland cells of the treated snails.

The reproductive rate ( $R_0$ ) and fecundity ( $M_x$ ) of adult *B. alexandrina* snails in the present study were significantly decreased by their exposure for four weeks to the sublethal concentrations of the tested compounds. These low values of  $R_0$  and  $M_x$  of treated snails could be attributed partially to their high mortality rates and different periods of ceasing egg-laying during the experimental period, in comparison with the control groups. Another assumption for this reduction in  $R_0$  of treated snails is the considerable deterioration in the activities of the enzymes AST and ALT in their tissues and hemolymph, which means damage to the snails' cells, hence interruption of their physiological activities, resulting in low or ceasing their opposition ( $M_x$ ) and net reproductive rate ( $R_0$ ). Also, this was confirmed by histological examination, which showed severe damage in the digestive and hermaphrodite gland cells of treated snails (Hasheesh & Mohamed, 2011). In addition, Mahmoud et al. (2011) attributed the effects partially to severe damage to the hermaphrodite gland cells of treated snails.

The present data revealed that hatchability rates of *B. alexandrina* eggs of older embryonic stages exposed for 24 hours to the sublethal concentrations  $LC_0$ ,  $LC_{10}$  and  $LC_{25}$  of these herbicides were higher than those of the freshly laid eggs, in which hatchability rate increased with increasing age and decreased with increased concentration of these herbicides. However, at  $LC_{90}$  from the tested compounds no eggs (1, 3 and 7 days old) hatched. The differences in susceptibility of the tested eggs to these compounds may be due to the ability of

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FIG. 8. Photomicrograph showing histological sections through hermaphrodite glands of treated snails with  $LC_{25}$  sublethal doses for two weeks (H & E). A: Amex 48% EC; B: Herphosate 48% SL; C: Stomp 50% EC. MO: Mature Ovum, SP: Sperm, SPR: Spermatocytes, OC: Oocyte, DO: Degenerated Ovum, DSP: Degenerated Sperms, V: Vacuole.



the tested herbicides to penetrate well the thick yolk layer of fresh laid eggs and to kill most of the few developing embryos within the exposed egg masses. Hasheesh et al. (2011) observed that freshly laid eggs more susceptible than older eggs to the fungicide Score. Youssef (2010) also recorded approximately similar effects of the pesticides Vertemic and Match on hatchability of *B. alexandrina* eggs.

Regarding the effect of the tested herbicides on *S. mansoni* miracidia and cercariae, our results indicate that mortality rates of these parasite larval stages were dependant on concentration and exposure period. Thus, these rates were increased by prolongation of the exposure period up to 180 min (three h) and by increasing the sublethal concentration used. This agrees with El-Emam et al. (2008) on the pesticides Regent, Mimic, Fenitrothion, Vertimec and Match against *S. mansoni* miracidia and cercariae. A similar conclusion was reached by Hasheesh & Mohamed (2011) against *S. haematobium* miracidia and cercariae exposed to the pesticides Chorpyifos and Profenofos, and they stated that the mortality rates of the miracidia and cercariae were elevated gradually by increasing the concentration of the tested pesticides. Abdel Raouf (2007) stated that the difference in mortality rates of both larval stages seems to be dependent on the chemical structure of the tested agents and not on the biological nature of these larvae.

Because all of the three herbicides in the present study induced histopathological changes of the digestive and hermaphrodite glands and the extent of damaged increased with an increase in the concentrations, the most prominent severe damage in the digestive cells was a great loss in shape of digestive cells (syncytium). The tips of digestive cells ruptured, and most of the cells were degenerated. Vacuoles and lumens inside tubule increased, and the secretory cells became denser in color and increased in number, and the connective tissue between digestive tubules shrank.

Our results agree with El-Deeb & El-Nahas (2005) on *Euphorbia nubica* and *Sesbania sesban* plants, which caused epithelial necrosis and abnormal increase in the ratio of secretory to digestive cells. Also, Bakry (2009) reported the same observations in the digestive gland of *B. alexandrina* past two weeks of exposure to LC<sub>25</sub> of *Guayacum officinalis*, *Atriplex stylosa* and *Euphorbia splendens* methanol extract.

In the present work, the histological examination of the hermaphrodite gland in treated snails showed loss of connective tissue, irregular sperm and mature ova appeared dense and irregular in shape after exposure to the three herbicides, and an acceleration in male gametogenic developmental stages were present in an obvious pattern after exposure to glyphosate isopropylammonium and Pendimethalin. These findings agree with the egg laying results, as the treated adult snails could lay eggs throughout the exposure period. These results agree with Al-Sharkawy et al. (1996), who observed gametogenic maturity acceleration in the hermaphrodite gland of *B. alexandrina* snails after exposure to *Ammi majus* dry plant powder. By increasing the concentrations of testing herbicides, the ova lost their normal shape, and the damage increased showing discharge, evacuation, detachment of some gonadal cells from acini and complete destruction of gametogenic cells. Moreover, the disappearance of most of the oocytes, spermatogenesis and connective tissues was evident. These observations were supported by the study of Hasheesh & Mohamed (2011), who attributed the reduction in egg laying of *Bulinus truncatus* treated with *Sesbania sesban* to severe histological damage to the snail's hermaphrodite gland cells and the evacuation of some of its tubules from various gametogenetic stages. This also agrees with a study by Mossalem et al. (2013) on the molluscicidal properties of the antihelminthic plant derivative, dihydro-artemisinin methyl ether (Artemether) against some histological and histochemical parameters of *B. alexandrina* snails, and they stated that there is a complete destruction of gametogenic cells and severe damage of hermaphrodite gland tissues, especially when the exposure period increased. From the previous results, it can be concluded that the three herbicides have a molluscicidal effect on the intermediate host of *Schistosoma mansoni*.

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EFFECTS OF INGESTION OF LITHIC PARTICLES ON GROWTH OF  
THE APPLE SNAIL *POMACEA CANALICULATA*  
(CAENOGASTROPODA, AMPULLARIIDAE)

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ABSTRACT

Lithic particles are a common feature in the digestive tract of freshwater snails. Their role in the digestive processes has been demonstrated in some microphytophagous and detritivorous species, as they enhance growth, assimilation and reproduction. It has been suggested that they could have the same function in *Pomacea canaliculata*, a macrophytophagous apple snail with powerful jaws and radula, a strongly muscular and cuticularized gizzard and high levels of enzymatic activity. Our aims were to investigate the occurrence of lithic elements in the digestive tract of *P. canaliculata* snails from natural populations through the analyses of digestive contents, as well as the effect of size and availability of lithic particles on growth and growth efficiency through laboratory experiments. Lithic particles are very common in the digestive tract of *P. canaliculata* from natural populations and from laboratory aquaria if they are available in the immediate environment. Such particles are not retained or concentrated differentially in the stomach and they are apparently totally lost in less than four weeks if the supply is interrupted. The frequency of plant material and lithic particles increases from mouth to anus indicating that the retention time increases in the same way. Sand and plant material frequently co-occur in the intestine and in the stomach indicating that both are ingested together. Ground marble had negative effects on the growth of *P. canaliculata* probably due to the sharp edges and pointed ends of these particles. The availability of natural lithic particles (sand) had a positive effect on growth and also a synergic interaction with the availability of food. The growth efficiency was 25.2% higher when sand was available than when it was absent. These effects were more marked in juvenile females than in juvenile males. Our results indicate that growth rates may be underestimated under laboratory conditions if lithic particles are not supplied regularly and that their presence should be standardized to allow reliable comparisons between studies. Our results also indicate that the effects of food availability and plant palatability on the growth of *P. canaliculata* may be modulated by the presence of lithic particles and this may in turn affect the outcome of interactions between apple snails, other snails and macrophytes.

Keywords: invader, feeding, digestion, trophic ecology, growth efficiency.

INTRODUCTION

Lithic particles are common in the digestive tracts of freshwater snails and they seem to play a role, in some cases essential, in the digestive processes of these animals (Dillon, 2000; Pyron & Brown, 2015). However, experimental tests of the effect of these particles on the growth, reproduction and assimilation have seldom been performed (e.g., Colton, 1908; Carriker, 1946; Noland & Carriker, 1946; Storey, 1970; Brendelberger, 1997; Thomas,

2001). Most of these studies were carried out on small sized pulmonates that are usually considered as microphytophagous and detritivorous grazer-scrapers thriving on algae, detritus and senescent plant material (Dillon, 2000; Pyron & Brown, 2015). On the other hand, apple snails (Ampullariidae) are large snails mostly with macrophytophagous habits (Cazzaniga & Estebenet, 1984; Cowie, 2002; Marchese et al., 2014; Hayes et al., 2015) and they possess very powerful jaws and radula with which they shred living macrophyte tissues

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(Andrews, 1965; Moretto & Nahabedian, 1989; Martín & Negrete, 2007). They also possess a strongly muscular and cuticularized gizzard in the stomach (Andrews, 1965) and high levels of enzymatic activity in different parts of their digestive tract (Godoy et al., 2013; Luo et al., 2015). Even though these mechanical and chemical tools seem to be sufficient enough to process the relatively soft tissues of the aquatic plants usually consumed, Andrews (1965) described the presence of “small stones or grit” in the gizzard of *Pomacea canaliculata* (Lamarck, 1822), and suggested that they play a role in the disintegration of vegetal material.

*Pomacea canaliculata* is one of the apple snails to which most records of negative impacts on aquatic crops and ecosystem functioning have been attributed (Cowie, 2002; Carlsson et al., 2004; Hayes et al., 2012; Horgan et al., 2014). Most of these impacts are caused directly by their ability to consume, grow and reproduce on a variety of aquatic plants, including semi-aquatic vascular plants that are difficult to ingest and digest due to their toughness (e.g., Boland et al., 2008; Wong et al., 2010). In spite of the relevant and negative impacts caused by the herbivory of *P. canaliculata* there are no specific studies about the occurrence of lithic particles in its digestive tract and their effect on the growth of this snail, which has been listed by the IUCN among 100 of the world’s worst invaders (Lowe et al., 2000). The main aims of the present study were to investigate the presence of lithic elements in the digestive tract of *P. canaliculata* from natural populations and to determine their significance in its trophic ecology. In particular, relative to trophic ecology, we investigated the effect of the size and availability of lithic particles on growth and growth efficiency.

## MATERIALS AND METHODS

### Field Sampling: Lithic Particles in Different Parts of the Digestive Tract

At least 20 adult snails with shell length (SL, measured from the apex to the farthest point on the aperture with a Vernier caliper to the nearest 0.1 mm) greater than 30 mm were collected by hand in three *P. canaliculata* populations from Southern Pampas (Buenos Aires province, Argentina): in El Huáscar stream (36°55'50"S, 61°35'48"W), in Guaminí stream (37°20'47"S, 62°25'20"W) and in an earthen

channel connecting Pigüé and Venado streams (37°11'26"S, 62°40'26"W).

The snails were sacrificed immediately in the field by sudden immersion in water at 80°C. In the lab the snails were stored at -18°C until they were processed. The snails were thawed and dissected. The digestive tract was split into three sections (crop, stomach and intestine; Fig. 1) which were analyzed separately in search of remains of plant material and lithic particles: sand (0.0625 to 2 mm) and fine gravel (2 to 4 mm).

Nine binary (presence-absence) variables resulting from the combination of the digestive content categories (S: sand, G: gravel and V: vegetal material) and the different sections of the digestive tract (C: crop, S: stomach, I: intestine) were established to analyze the digestive contents; the variables were named accordingly (e.g.: SC: sand in the crop). A cluster analysis was performed using the Jaccard coefficient and the median linkage method to show the association between the variables.

### Origin and Maintenance of Snails for Laboratory Experiments

All the snails used in the experiments were obtained from egg masses deposited in the

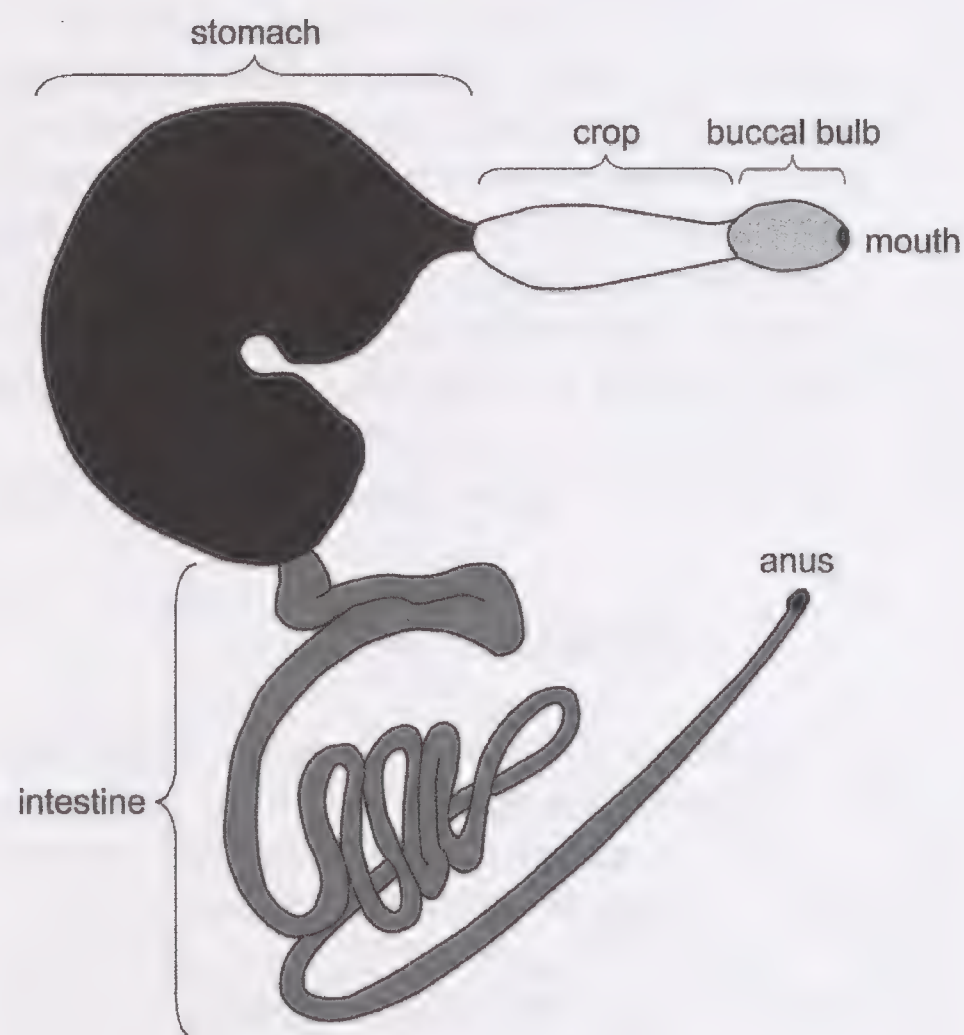


FIG. 1. Scheme of the digestive tract of *P. canaliculata* adults, indicating the different sections of which the contents were analyzed in the present study (crop, stomach and intestine).



laboratory by a stock of snails from El Huáscar stream. The experimental snails were reared since hatching in individual 200 mL plastic aquaria with  $\text{CaCO}_3$ -saturated tap water at 25°C, with a 14:10 h (light:dark) photoperiod, and they were fed with lettuce *ad libitum*. The aquaria were cleaned and the water changed once a week.  $\text{CaCO}_3$ -saturated tap water was used during the rearing phase to ensure the integrity of the shell. Once the experiments on the snails were started they were transferred to individual 3 L aquaria with non  $\text{CaCO}_3$ -saturated tap water to avoid interference of  $\text{CaCO}_3$  precipitate with the lithic particles.

#### Growth Determinations in Laboratory Experiments

All the experiments lasted for four weeks but lithic particles were available since the previous week (week zero; see below). Juvenile snails (between 15 and 20 mm in shell length) were used in all the experiments ( $n = 10$  in each treatment, including controls). At the start of each experiment (end of week zero) the initial shell length ( $SL_0$ , mm) of the snails was measured as above and the initial live weight ( $LW_0$ , g) was obtained with a digital scale ( $\pm 1.0$  mg) after allowing the snails to crawl in a plastic container without water for 30 min to assure the loss of most of the water from the mantle cavity. These measurements were repeated weekly until the fourth week of each experiment.

At the end of the experiments the snails were sacrificed by sudden immersion in boiling water. The snails were stored at -18°C until they were processed. The shell and operculum were removed (except in Experiment 1; see below) and the soft parts were weighed after 72 h at 60°C to obtain their dry weight (SPDW, g). Although the snails were sexually undifferentiated at the start of the experiments, they were dissected before drying and the sex was determined by observation of the penis sheath (males) or the albumen gland (females). The ash content of the soft parts was obtained after 4 h at 600°C and the ash free dry weight (AFDW, g) was calculated.

#### Experiment 1: Effect of Availability of Lithic Particles

In this experiment ground marble was chosen as a substitute for natural lithic particles due to its mineralogical and granulometric homogene-

ity. Its whitish color also made it easier to detect among the digestive contents and feces, which are usually dark green-brown in this species (Castro-Vazquez et al., 2002). Commercial ground marble was sieved and washed with water before use to obtain particles of similar size ( $1.285 \pm 0.075$  mm, mean  $\pm$  SE) and free of dust.

We used three treatments to study the effect of the availability of lithic particles on the growth of juvenile snails fed *ad libitum*: continuous (CA), discontinuous (DA) and no availability (NA, control) of lithic particles. In the DA treatment the lithic particles were only available during week zero: 2–2.5 cm<sup>3</sup> of ground marble were added after the last water change in the 200 mL aquaria. In the CA treatment the ground marble was provided in the same way during week zero but, after the change to the 3 L aquaria, 2–2.5 cm<sup>3</sup> of ground marble were also added every week after the water change.

After the freezing period the soft parts of the snails were removed from the shell and dissected to investigate the presence of ground marble in the stomach and intestine (Fig. 1); the feces at the bottom of the aquaria were also inspected in search of marble particles. Afterwards, the shell and soft parts (including the operculum) were dried for 72 h at 60°C and weighed together to obtain the total dry weight (TDW, g).

#### Experiment 2: Effect of Size and Availability of Lithic Particles

In this experiment sieved sand obtained from the Napostá stream (38°41'56"S, 62°15'57"W, Buenos Aires province, Argentina) was used. The sand was thoroughly washed in flowing tap water to eliminate the least dense elements (organic debris and pieces of shells) by flotation and drift. The sand was sieved through a series of meshes to obtain two fractions of different diameter (mean  $\pm$  SE):  $0.80 \pm 0.05$  and  $1.69 \pm 0.05$  mm (coarse sand and very coarse sand, respectively, according to the Wentworth scale).

Five treatments were designed to test for the effect of size and availability of lithic particles on the growth of juveniles fed *ad libitum*: no availability of lithic particles (NA, control), discontinuous availability of small (DAS) and large lithic particles (DAL) and continuous availability of small (CAS) and large lithic particles (CAL). Lithic particles in the discontinuous availability treatments were only available during week



zero (2–2.5 cm<sup>3</sup> of sand were added after the last water change in the 200 mL aquaria), as in Experiment 1, while in the continuous availability treatments the same amount of sand was also added every week after the water change in the 3 L aquaria.

### Experiment 3: Effects of Availability of Lithic Particles and Food and their Interaction

In this experiment washed and sieved sand obtained from the Napostá stream was also used. The sand was washed as above and sieved through a series of meshes to obtain a fraction between  $1.225 \pm 0.05$  mm (very coarse sand).

To test for the effects of availability of food and lithic particles on the growth and growth efficiency of juvenile snails, four treatments were performed with a factorial design: food availability (FA) x lithic particles availability (LPA). Two levels of food availability were set: 100% and 50% of the *ad libitum* ingestion of lettuce (FA 100% and FA 50% respectively). The amount of food in week  $i$  ( $F_i$ , provided in two doses) was estimated on the basis of  $SL_{i-1}$  (previous week) using the allometric equation developed by Tamburi & Martín (2009b) for *P. canaliculata* daily ingestion rates. Two levels of availability of lithic particles were used: no availability (NA) and continuous availability (CA); in the latter, 2–2.5 cm<sup>3</sup> of sand were added after the last water change in the 200 mL aquaria and every week after the water change in the 3 L aquaria.

Growth efficiency in live weight (GELW, g g<sup>-1</sup>) was estimated on the basis of the increase in live weight and the accumulated amounts of food provided each week ( $F_i$ , g):  $GELW = (LW_4 - LW_0) / (F_1 + F_2 + F_3 + F_4)$  throughout the experiment.

### Statistical Analysis of Experimental Data

The data from the laboratory experiments were analyzed through one-way ANOVAs (Experiment 1 and Experiment 2) and two-way ANOVAs (Experiment 3). Levene's test was previously performed to investigate homoscedasticity; when homogeneity of variances was rejected for a given variable, the data corresponding to that variable were transformed (see Results). If no transformation was able to homogenize the variances of that variable, the data were analyzed through Kruskal-Wallis tests in the Experiment 1 and in Experiment 2;

in the case of Experiment 3, the factorial design was split by food availability for some variables (see Results) and the difference between snails with and without sand was analyzed by Kruskal-Wallis tests. Fisher's LSD test (least significant difference test) was performed to locate differences between means.

In some experiments the Levene's test and graphical analyses of data suggested that there were differences between the juvenile snails that were already sexually differentiated. In such cases, we split the data and each sex was analyzed separately as above.

## RESULTS

### Field Sampling: Lithic Particles in Different Parts of the Digestive Tract

The majority of the individuals dissected (93.6%) had lithic particles at least in one section of their digestive tracts. The digestive contents in the three populations were quite similar; the main overall pattern was an increase in the three categories of contents from mouth to anus (Fig. 2). The frequency of lithic particles in the stomach was lower than in the intestine, whereas that of vegetal material was almost the same. Gravel was always the least represented category throughout the digestive tract.

The association in the presence of sand and vegetal material was high both in the intestine and in the stomach and it was also quite similar between these two sections of the

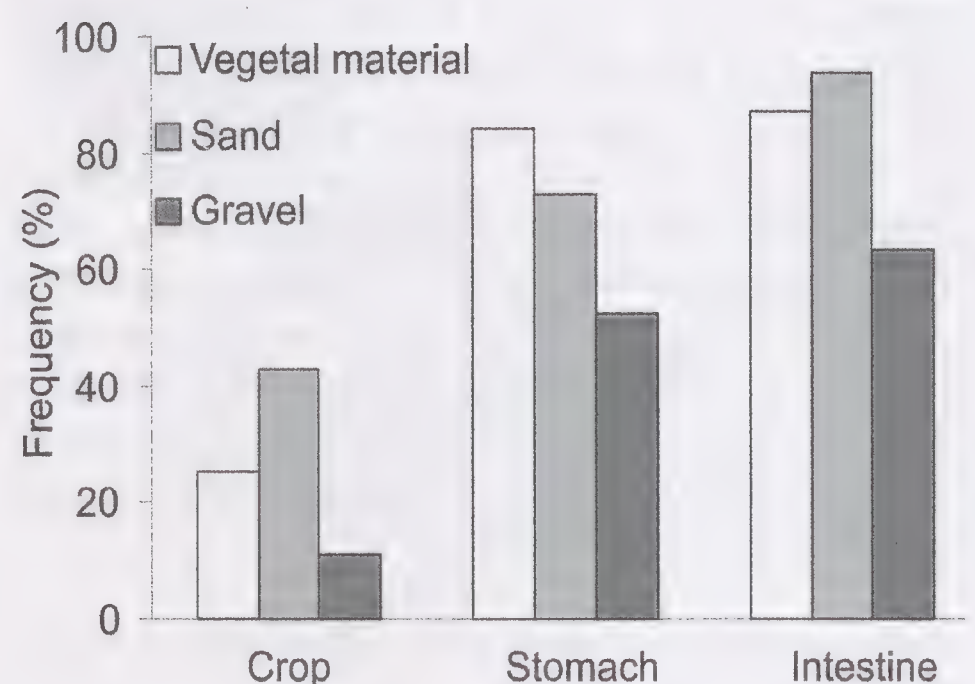
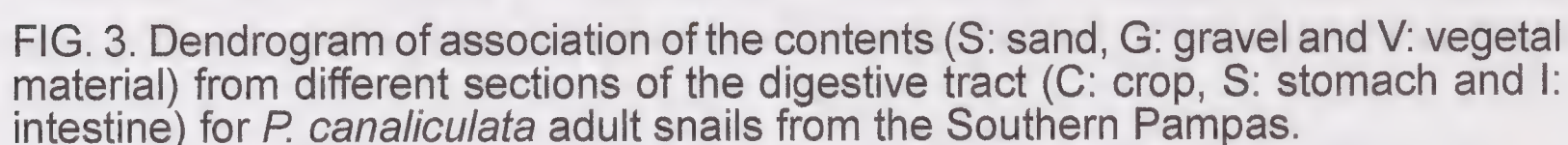


FIG. 2. Frequency of occurrence of vegetal material and lithic particles (sand and gravel) in different sections of the digestive tract for *P. canaliculata* adult snails from the Southern Pampas.



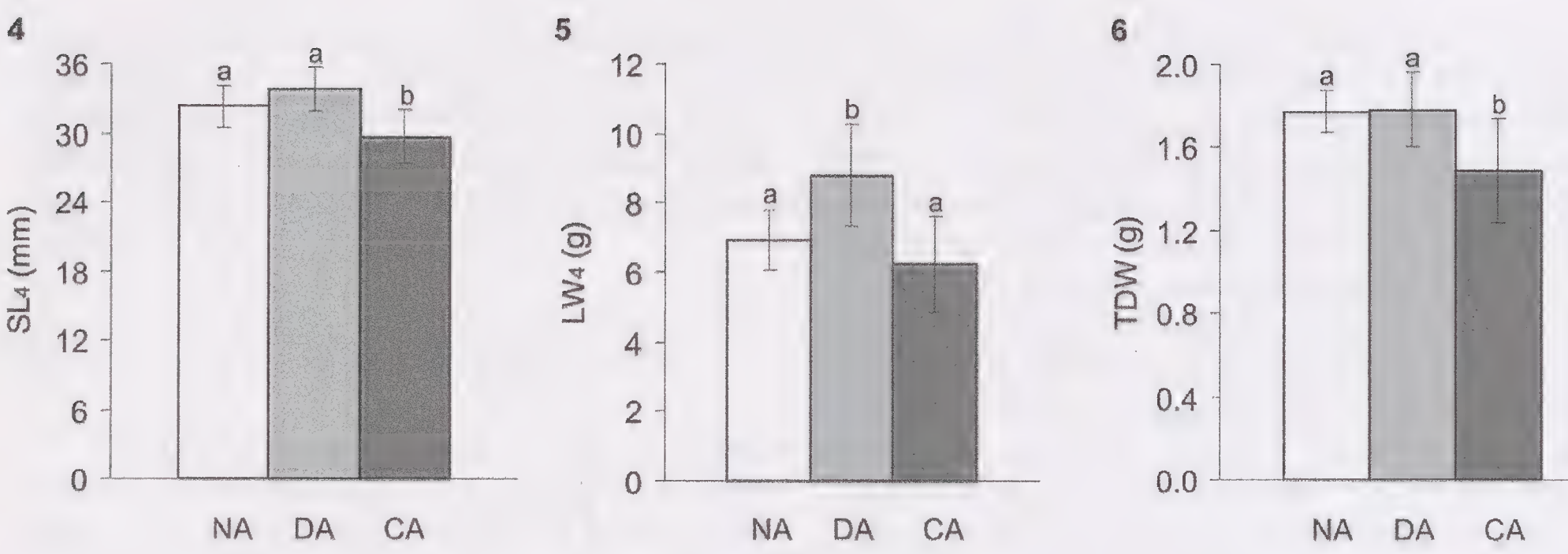


The effect of ground marble on the growth of *Pomacea canaliculata* was mostly negative (Table 1; Figs. 4–6): the snails with continuous availability of ground marble (CA) showed significantly lower final values of SL and TDW than the other two treatments. The final LW of the discontinuous availability treatment (DA) was significantly higher than the control without any marble (NA) and the continuous availability one (CA). When males and females were analyzed separately the negative effects of ground marble on the final values of SL, LW and TDW were not significant (males: SL ( $F_{2,19} = 2.967$ ;  $p = 0.076$ ), LW ( $F_{2,19} = 1.811$ ;  $p = 0.191$ ) and TDW ( $F_{2,19} = 2.179$ ;  $p = 0.141$ ); in the case of females, t-tests for unequal variances were performed as there were no females in the control: SL ( $t_{2,255} = 1.429$ ;  $p = 0.276$ ), LW ( $t_{2,195} = 1.655$ ;  $p = 0.229$ ) and TDW ( $t_{2,217} = 1.711$ ;  $p = 0.217$ )).

No significant effects of size and availability of lithic particles were detected on  $SL_4$  ( $F_{4,45} = 0.376$ ;  $p = 0.825$ ),  $LW_4$  ( $F_{4,45} = 0.354$ ;  $p = 0.840$ ),  $SPDW$  ( $F_{4,45} = 0.161$ ;  $p = 0.957$ ) and  $AFDW$  ( $F_{4,45} = 0.265$ ;  $p = 0.899$ ). The dissections performed after the experiment showed that 45 out of 50 experimental snails were juvenile males.

|                 | F <sub>2;27</sub> | p-value | MS Error |
|-----------------|-------------------|---------|----------|
| SL <sub>4</sub> | 5.318             | 0.011   | 7.933    |
| LW <sub>4</sub> | 5.596             | 0.009   | 3163461  |
| TDW             | 3.983             | 0.030   | 68797    |





FIGS. 4–6. The effect of availability of lithic particles on growth of juveniles of *P. canaliculata* (mean  $\pm$  95% CI); no availability (NA), discontinuous availability (DA), continuous availability (CA). FIG. 4: Final shell length (SL<sub>4</sub>); FIG. 5: Final live weight (LW<sub>4</sub>); FIG. 6: Total dry weight (TDW). Treatments with the same letter were not significantly different ( $p > 0.05$ ) after Fisher's LSD test.

Experiment 3: Effects of Availability of Lithic Particles and Food and their Interaction

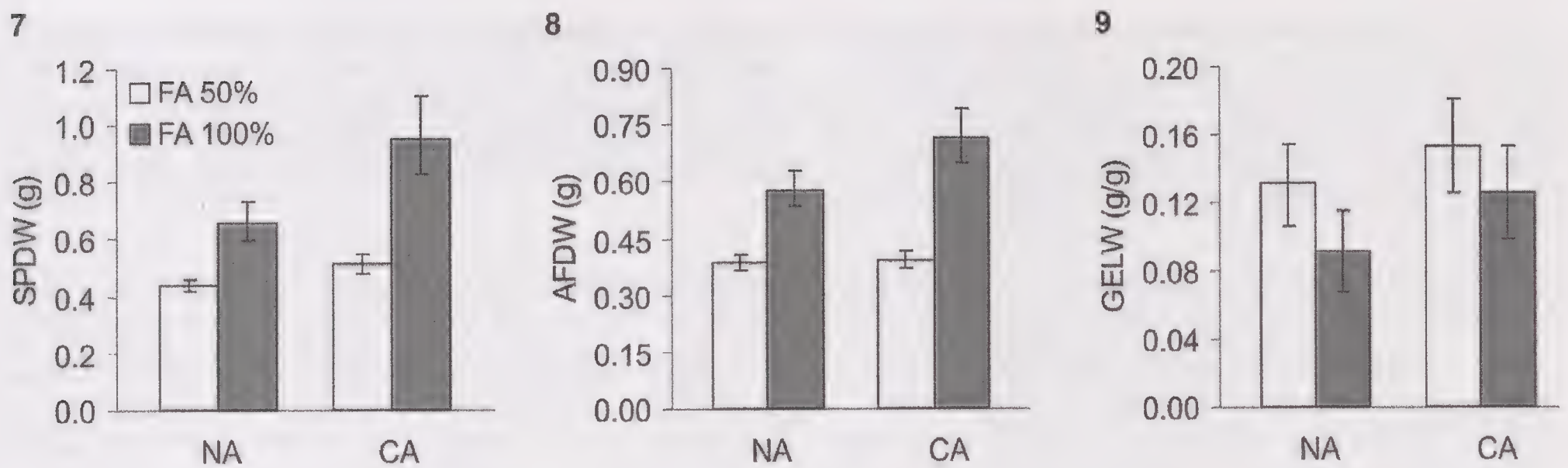
The effects of food availability and lithic particles on the final values of SL, LW, SPDW and AFDW were significant and positive (Table 2; Figs. 7–11); the interaction of the two factors was also significant and positive. The SPDW of snails fed *ad libitum* was 44.5% higher when lithic particles were available to them

whereas their effect on snails with reduced food availability was only 17.3% (Fig. 7). The corresponding comparative values for AFDW (Fig. 8), SL<sub>4</sub> (Fig. 10) and LW<sub>4</sub> (Fig. 11) were 23.6 vs. 2.4%, 17.3 vs. 4.8% and 53.8 vs. 15.3%, respectively. The synergistic effect of food and lithic particle availability on the latter two variables was already apparent in their respective growth curves in week one (Figs. 10, 11) but they increased with time until the

TABLE 2. Two-way ANOVAs for the effect of lithic particle (LPA) and food availability (FA) and their interaction (FA x LPA) on growth and growth efficiency of juveniles of *P. canaliculata*. Abbreviations: final shell length (SL<sub>4</sub>), final live weight (LW<sub>4</sub>), soft parts dry weight (SPDW), ash free dry weight (AFDW), growth efficiency in LW (GELW). SPDW and AFDW were logarithmically transformed.

|                 |                   | LPA    | FA      | FA x LPA | MS Error |
|-----------------|-------------------|--------|---------|----------|----------|
| SL <sub>4</sub> | F <sub>1,36</sub> | 12.362 | 14.490  | 4.246    | 7.378    |
|                 | p-value           | 0.001  | 0.000   | 0.047    |          |
| LW <sub>4</sub> | F <sub>1,36</sub> | 15.815 | 22.532  | 6.182    | 1631464  |
|                 | p-value           | 0.000  | 0.000   | 0.018    |          |
| SPDW            | F <sub>1,36</sub> | 37.037 | 142.789 | 5.784    | 0.004    |
|                 | p-value           | 0.000  | 0.000   | 0.021    |          |
| AFDW            | F <sub>1,36</sub> | 12.661 | 232.055 | 8.077    | 0.002    |
|                 | p-value           | 0.001  | 0.000   | 0.007    |          |
| GELW            | F <sub>1,36</sub> | 6.038  | 8.462   | 0.267    | 0.001    |
|                 | p-value           | 0.019  | 0.006   | 0.609    |          |





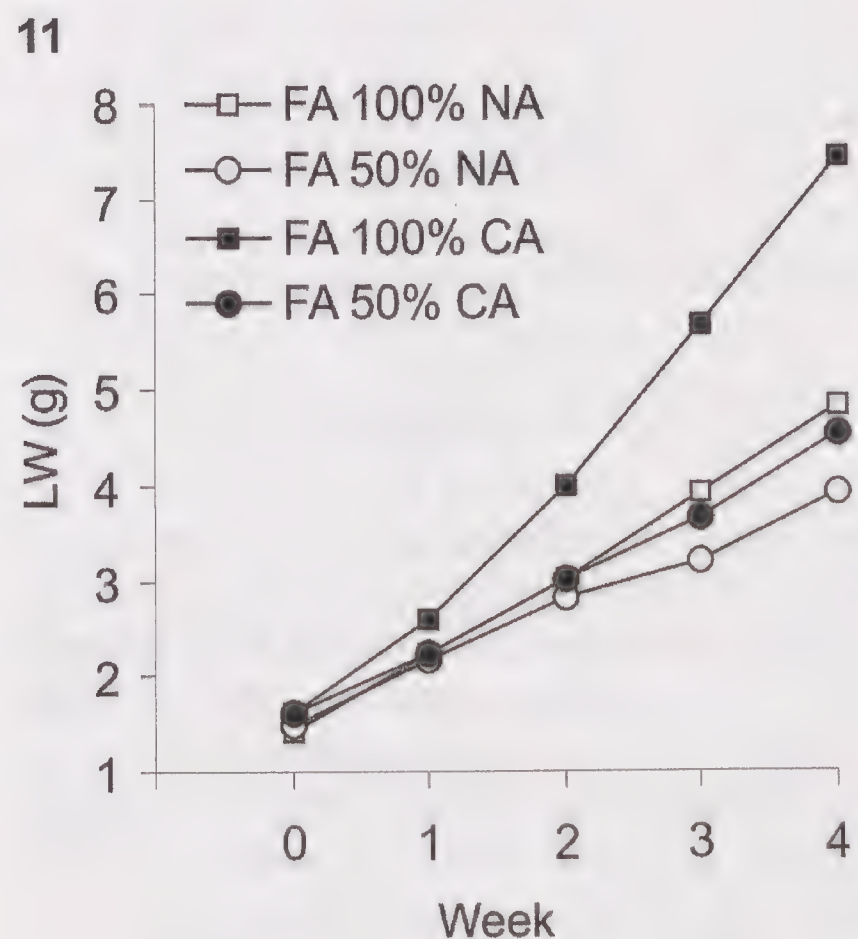
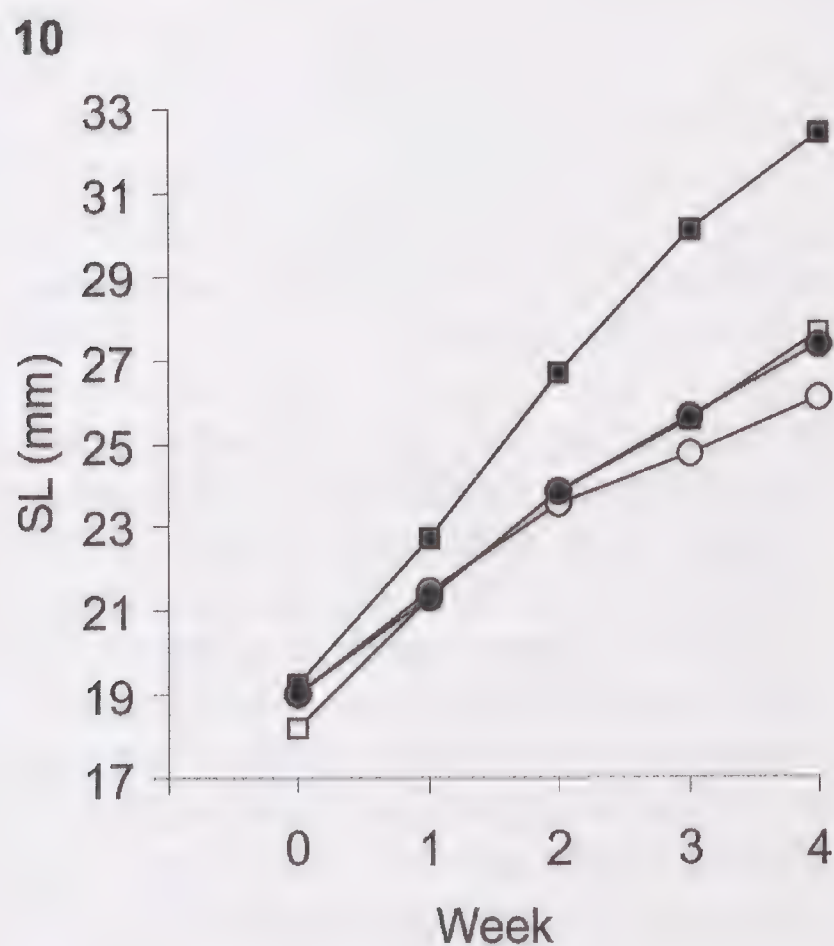
FIGS. 7–9. The effect of availability of lithic particles (NA, no availability and CA, continuous availability) and food (FA 100% and FA 50%) on growth and growth efficiency of juveniles of *P. canaliculata* (mean  $\pm$  95% CI). FIG. 7: Soft parts dry weight (SPDW); FIG. 8: Ash free dry weight (AFDW); FIG. 9: Growth efficiency in LW (GELW).

end of the experiment. The availability of lithic particles allowed the snails with 50% food availability to grow at the same rate as those with 100% food availability but without lithic particles.

On the other hand, the growth efficiency in LW (GELW) showed a significantly positive effect of lithic particles and a significantly negative effect of food availability but there was no significant interaction between these two factors (Table 2; Fig. 9). The GELW of snails fed *ad libitum* and under reduced availability was, on average, 25.2% higher when sand was available than when it was not. The average

GELW of snails fed *ad libitum* was 15.0% lower than the corresponding values of snails with 50% reduction in food availability.

The pattern of the effects of food and lithic particle availability and their interaction on  $SL_4$ ,  $LW_4$ , SPDW, AFDW and GELW was the same for juvenile females when they were analyzed separately (Table 3); when lithic particles were available and food availability was low the GELW of females was, on average, 12.0% higher whereas it was 9.0% lower for females fed *ad libitum*. In the case of males, only  $SL_4$  showed a significantly positive effect of food when they were analyzed alone.



FIGS. 10, 11: The effect of availability of lithic particles (NA, no availability and CA, continuous availability) and food (FA 100% and FA 50%) on growth of juveniles of *P. canaliculata*. FIG. 10: Mean shell length (SL); FIG. 11: Mean live weight (LW).



TABLE 3. Two-way ANOVAs for the effect of lithic particle availability (LPA) and food availability (FA) and their interaction (FA x LPA) on growth and growth efficiency of juvenile females and males of *P. canaliculata*: final shell length (SL<sub>4</sub>), final live weight (LW<sub>4</sub>), soft parts dry weight (SPDW), ash free dry weight (AFDW) and growth efficiency in LW (GELW). SPDW was logarithmically transformed for females and SL<sub>4</sub> was inversely transformed for males. X<sup>2</sup> values are shown when Kruskal-Wallis tests were performed for the effect of LPA only.

|         | Variable        | Statistic                   | LPA    | FA      | FA x PA | MS Error |
|---------|-----------------|-----------------------------|--------|---------|---------|----------|
| Females | SL <sub>4</sub> | X <sup>2</sup> <sub>1</sub> | 4.644  |         |         |          |
|         |                 | p-value                     | 0.031  |         |         |          |
|         | LW <sub>4</sub> | F <sub>1;22</sub>           | 39.524 | 141.725 | 10.901  | 283656   |
|         |                 | p-value                     | 0.000  | 0.000   | 0.003   |          |
|         | SPDW            | F <sub>1;22</sub>           | 98.917 | 373.373 | 8.079   | 0.001    |
|         |                 | p-value                     | 0.000  | 0.000   | 0.009   |          |
|         | AFDW            | F <sub>1;22</sub>           | 23.153 | 241.169 | 10.741  | 2120     |
|         |                 | p-value                     | 0.000  | 0.000   | 0.003   |          |
|         | GELW            | F <sub>1;22</sub>           | 9.904  | 20.042  | 0.16    | 0.000    |
|         |                 | p-value                     | 0.005  | 0.000   | 0.693   |          |
| Males   | SL <sub>4</sub> | F <sub>1;10</sub>           | 2.007  | 5.533   | 0.542   | 0.000    |
|         |                 | p-value                     | 0.187  | 0.040   | 0.478   |          |
|         | LW <sub>4</sub> | X <sup>2</sup> <sub>1</sub> | 0.538  |         |         |          |
|         |                 | p-value                     | 0.463  |         |         |          |
|         | SPDW            | X <sup>2</sup> <sub>1</sub> | 0.360  |         |         |          |
|         |                 | p-value                     | 0.549  |         |         |          |
|         | AFDW            | X <sup>2</sup> <sub>1</sub> | 1.604  |         |         |          |
|         |                 | p-value                     | 0.205  |         |         |          |
|         | GELW            | X <sup>2</sup> <sub>1</sub> | 0.111  |         |         |          |
|         |                 | p-value                     | 0.739  |         |         |          |

DISCUSSION

The results obtained in the present study showed that lithic particles are very common in the digestive tract of *Pomacea canaliculata* whenever they are available in the immediate environment. The presence and the characteristics of these lithic particles affect the growth efficiency and the size attained by juvenile snails, especially by the females.

The presence of gravel in all sections of the digestive tract of snails from the natural populations indicates that these particles are not retained or concentrated differentially in the stomach, as Andrews' (1965) observations seemed to suggest. Lithic particles have been

found at high frequencies but with low abundances in the digestive tract of *P. canaliculata* (Kwong et al., 2010; Ocon et al., 2013; López van Oosterom et al., 2013). The frequency of vegetal material, sand and gravel increases from mouth to anus, probably indicating that the retention time in each section also increases in the same way. The crop seems to be the site of short term accumulation of ingested material during bouts of feeding. *Pomacea canaliculata* shows a slightly higher level of activity (Heiler et al., 2008) and of pedal collection of water surface food during the night (Saveanu & Martín, 2013), which may explain why most crops were empty during our diurnal sampling. The intestine is apparently not only



a site of absorption but also of digestion, since proteases are freed to its lumen (Godoy et al., 2013), and this function may be related to an extended retention time relative to other parts of the digestive tract.

The high association of sand and plant material in the intestine and in the stomach probably indicates that the sand was deposited on the plant material and both were ingested together. On the other hand, the presence of gravel in the intestine and the stomach was quite independent of the other two items, probably due to its lower association with plant material. The low degree of association of the crop contents with that of other section is probably due to the high percentage of empty crops. The crop contents only reflect the feeding history of the snail during the few hours prior to collection, whereas those of the stomach, and especially the intestine, integrate the food ingested over several days previous.

The effect of ground marble on growth of *P. canaliculata* was unexpected since the snails with continuous availability attained significantly lower values of shell length and dry weight. In the case of dry weight, the negative effect overcame the additional weight of marble particles in the digestive tract since the dissections showed that the snails with continuous availability still contained these particles in their digestive tracts at the end of the experiment. In the case of final live weight, the effect was inconsistent as under discontinuous availability the snails grew significantly more than in the controls, or than snails under continuous availability. This cannot be explained by the added weight of the marble particles since the dissections showed no particles in their digestive tracts after the four weeks of the experiment.

Accounts of negative effects of lithic particles are rare in the literature. For instance, Schmölder & Becker (1990) found greater shell growth rates and production of eggs and egg reserves during four weeks in snails without sand as compared to those with it although later the differences disappeared despite the active ingestion of sand by *Biomphalaria glabrata* (Say, 1818). The negative effects of ground marble in the case of *P. canaliculata* were probably due to injuries to, or clogging of, the digestive tract because of the irregular and flattened shape and the sharp edges and pointed ends of these particles. The fact that our snails ingested ground marble in spite of its negative effects supports the idea that at least some of the lithic particles are ingested accidentally during feeding. The marble par-

ticles were clearly different from those present in natural waterbodies (mostly rounded and smooth) and found in the digestive contents or used in the other two experiments. The opposite effects of lithic particles described in two studies on *B. glabrata* (Schmölder & Becker, 1990; Thomas, 2001) may be due to differences in mineralogy, size and shape of the particles used in the experiments.

The effect of availability of natural lithic particles (sand) on all the variables related to the somatic growth of *P. canaliculata* (SL<sub>4</sub>, LW<sub>4</sub>, SPDW and AFDW) was significant and positive. This positive effect has also been described in different species of freshwater pulmonate snails (Colton, 1908; Carriker, 1946; Noland & Carriker, 1946; Storey, 1970; Brendelberger, 1997; Thomas, 2001), which also ingest selectively and retain sand grains. Three main mechanisms have been suggested to explain these positive effects: an increase in the mechanical digestion of food, an increase in the availability of micronutrients and the digestion of microbiota inhabiting the sand grains (Thomas, 2001). The last hypothesis seems implausible in our case since the sand grains were thoroughly washed and then maintained dry until use and were renewed weekly.

The growth efficiency of snails when sand was available was 25.2% higher than when it was absent. This increase in growth efficiency seems too high to be explained only by the effect of micronutrients. Probably the presence of sand allowed a greater breakdown of vegetal tissues and cells, as was suggested by Andrews (1965), and hence a higher efficiency in the extraction of intracellular organic compounds and perhaps a greater relative surface area for the action of digestive enzymes (Godoy et al., 2013; Luo et al., 2015).

The presence of sand had a synergistic effect with food availability on the growth rates of *P. canaliculata* juveniles, especially for females. Under low food availability the digestive efficiency was higher, as indicated by the high values of growth efficiency, but the total effect on growth was low due to the scarce amount of food available. On the other hand, when food availability was high the digestive efficiency was probably lower but the addition of sand allowed a more complete disintegration, which coupled with the abundant vegetal material allowed a multiplicative effect on the growth rates.

In the case of the juvenile males of *P. canaliculata* in the third experiment, the presence of sand had no effect and the food availability



only provoked an increase in shell length. In this case the lack of significant effects may be due to the small number of replicates but this is not the case in the second experiment. In the second experiment no effect of the size of lithic particles or its availability was found, probably due to the fact that 90% of the juveniles were males, an odd result but compatible with the oligogenic sex-determination mechanism in this species (Yusa, 2007). The males of *P. canaliculata* have lower growth rates than females even before maturity is attained (Estoy et al., 2002; Estebenet & Martín, 2003; Tamburi & Martín, 2009a) and so the experimental error in the estimations of male growth would have been proportionally higher. On the other hand, the digestive gland of males is 28–39% smaller than that of females (Vega et al., 2005) due to a greater portion of the visceral mass being occupied by the testicle than by the ovary, which may have impeded them from taking advantage of the higher disintegration of food.

*Pomacea canaliculata* females apparently profit more than males from the presence of sand. This species is usually dimorphic in shell size, with females attaining large sizes more frequently than males (Cazzaniga, 1990; Estebenet & Martín, 2002; Tamburi & Martín, 2009a). However, the differences in size between sexes differ notably among populations (Estebenet et al., 2006), probably due to the sexually dimorphic reaction norms to food availability (Tamburi & Martín, 2009a). Perhaps the variation in the availability and composition of particles among sites enhances or diminishes the size dimorphism between sexes due to different effects on the growth rates of both sexes.

Several studies showed that although apple snails are generalist herbivores they feed selectively and grow differently on diverse macrophytes (Estebenet, 1995; Lach et al., 2000; Morrison & Hay, 2011), in part due to the differences in the mechanical defenses of the latter (Boland et al., 2008; Wong et al., 2010). Experiments using reconstituted plants showed that the physical defenses negatively affect the ingestion rates of *P. canaliculata* (Wong et al., 2010). This may be attributed to the difficulties in chewing and shredding the tissues of plants with high dry matter content, although a hindrance to the mechanic digestion along the digestive tract may also be important. Storey (1970) mentioned that *Radix peregra* (Müller, 1774) eats aquatic macrophytes more readily and at a higher rate when sand grains are

present. Probably some plants that appeared to promote little growth, survival and fecundity in *P. canaliculata* (Qiu & Kwong, 2009) would have had more beneficial effects if lithic particles have been available. Brendelberger (1997) found that the addition of sediment increases the growth of two freshwater snails when feeding on certain trophic items (diatoms, green algae and maple leaf particles) but not when feeding on others (blue green algae).

In the third experiment the final sizes attained by the snails fed *ad libitum* were 17.3 to 53.8% higher when sand was available. These results indicate that the growth rates estimated for *P. canaliculata* in most laboratory studies (e.g., Tamburi & Martín, 2009b; Seuffert & Martín, 2013) were in fact underestimations of the maximum growth rates that this snail can reach under *ad libitum* conditions. Other studies used shell oyster powder or coral sand to provide calcium to apple snails (e.g., Estoy et al., 2002; Garr et al., 2011) and probably these materials play the role as lithic particles. However, the sign and magnitude of the effects may depend on the size and shape of the shell or coral fragments used, as our experiment with ground marble showed. These results indicate that the presence of lithic particles should be standardized as well as other details of the rearing conditions, in order to allow meaningful comparisons between studies on apple snail biology.

As in other freshwater snails, the lithic particles have a quantitatively important effect on growth and probably also on reproduction but they cannot be considered as essential (but see Storey, 1970). For instance, in *P. canaliculata* the availability of lithic particles allowed the snails to compensate for reductions in food availability up to 50%, indicating their importance in waterbodies where availability is naturally low or fluctuating or where it has been reduced by the herbivory of the apple snails on the submerged macrophytes (e.g., Carlsson et al., 2004). On the other hand, negative effects of lithic particles appear under certain circumstances (our study; Schmölder & Becker, 1990). The magnitude and sign of species interactions frequently vary according to the abiotic and biotic context (Chamberlain et al., 2014; Früh et al., in press). Our results indicate that the outcome of interactions among apple snails and other snails, and also with macrophytes, may be modulated by the effects of the sediment traits (size, shape and mineralogy) on the growth and reproduction of the snails.



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## *PUPILLA ALLUVIONICA* MENG & HOFFMANN, 2008: A LAND SNAIL EXTANT IN THE ALTAI REFUGIUM RECOGNISED FOR THE FIRST TIME IN CENTRAL EUROPEAN EARLY-MIDDLE PLEISTOCENE GLACIALS

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### ABSTRACT

*Pupilla alluvionica* Meng & Hoffmann, 2008 is an extant land snail species known until now only from a few sites in the Russian Altai Mountains. We have now identified it in fossil loess assemblages of Early-Middle Pleistocene age at three Central European sites. Fossil materials match those of Altaian populations, being only slightly smaller in mean shell width. In addition to the details of the locations and biometrics of these fossil finds, we list the faunas associated with *P. alluvionica* in the deposits. These are compared with the ecological conditions and associated faunas of living populations from the Altai. *Pupilla alluvionica* is a typical inhabitant of xeric habitats: steppes with rocky limestone outcrops. This matches the known habitat preferences of associated species in the fossil deposits that are typical of open loess steppe.

Key words: Altai refugium, Brunhes-Matuyama reversal, Central Europe, first record, land snails, loess, Pleistocene.

### INTRODUCTION

During the Quaternary of Europe there were repeated shifts in species ranges reflecting the climatic and associated habitat changes through each glacial/interglacial cycle (e.g., de Lattin, 1967; Ložek, 1976; Stewart et al., 2010; Schenková et al., 2013). Many land snail species of the European Pleistocene were originally described and known only from the fossil record from Central Europe (Ložek, 1954, 1964). Subsequently, some of them were discovered extant in locations far from Europe; in particular, several species characteristic of Central European loess deposits have been discovered living in the mountain ranges of Central Asia (Meng & Hoffmann, 2009; Horsák et al., 2010a). The Altai Mountains of southern Siberia appear to offer the best modern analogue of the Quaternary loess steppe environment of Central Europe (Horsák et al., 2010a, 2015; Hoffmann et al., 2011). With just one exception, all characteristic snail species of loess deposits (*sensu* Ložek, 2001) were recorded in this area, and some assemblages, living in areas of microclimate resembling that

estimated for the full-glacial of Central Europe had very similar assemblages to those of the latter in terms of species composition (Meng, 2008; Horsák et al., 2010a, 2015).

Among the species recorded in the Altai was a species new to science, *Pupilla alluvionica* Meng & Hoffmann, 2009. In reviewing previously reported loess faunas from Central Europe, we noticed that one species, described by Ložek (1969) as “a robust form of *Pupilla muscorum*” appeared to be very similar to this newly described and extant species. In this paper we provide the evidence that this “robust form” from three Central European sites is in fact *P. alluvionica*, and we discuss the similarities in associated faunas and what this identification tells us about the paleoenvironment prevailing when these deposits were laid down.

### MATERIALS AND METHODS

The three loess series involved (Fig. 1) have been regarded as classical old Pleistocene sites. Stránská skála and Červený kopec near Brno (Czech Republic) belong to the Cromerian and older complex (Prošek & Ložek, 1957;

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Musil, 1965; Kukla, 1975, 1977; Ložek, 2001). Loess rich in shells underlies foot-slope scree sequences of a Cromerian interglacial dated by the palaeontological evidence (Biharian zone of *Mimomys savini*; Horáček & Ložek 1988).

The limestone outcrop hill of Stránská skála is located at the southeast margin of Brno. The Brunhes-Matuyama reversal indicating an age older than 781 kyr lies in the uppermost part of the loess about 5.5 m below the early interglacial calcareous sinter with *Helicigona capeki* (Petrbok, 1922) and *Zonitoides sepultus* Ložek, 1964 (Prošek & Ložek, 1957; Kukla, 1975, 1977). The sequence sampled here represents a 13 m high talus-slope profile of fossil soils and sediments (for lithology: Kovanda, 1995). Notably large *Pupilla* specimens were found in the upper meter of pure loess layer underlying the Cromerian talus slope deposits (unpublished material collected by V. Ložek, 04.08.1991).

The Červený kopec site is an abandoned loess quarry and a former brickyard situated in southwest part of Brno. The section at the Červený kopec consists of a loess/paleosoil sequence, including 17 interglacial/glacial cycles, which was investigated in detail by Kukla (1975, 1977). Thick loess sediments are overlain by the soils of Kukla's PK IX and X (ca 0.8 Myr), representing two paleosoil sequences below the Brunhes-Matuyama reversal (for the stratigraphy and position of samples see Kukla 1977). Notably large *Pupilla* specimens were found in pure loess assemblages in the base of PK X (unpublished material collected by V. Ložek, 26.07.1970) from three different samples.

Krems an der Donau (Austria) is even older than the two above-mentioned sites (Kukla 1975, 1977; Fink, 1976; Fink et al., 1978). The Krems-Schiesstatte site is situated in a hilly transition area between the Bohemian Massif and the Molasse Basin. It is an exposure in a loess fill of an abandoned river meander with the elevation of 60 m above the Danube River. The profile up to 35 m thick includes approximately 15 paleosoils labelled KR 1-15 from the top to bottom; the Matuyama-Brunhes reversal was detected between KR 5 and KR 4 and all five loess sediments with large *Pupilla* specimens are situated below KR 9 and lower (for the stratigraphy and samples situation: Fink et al., 1978).

In the Altai Mountains, sampling plots of 10 m x 10 m were located in the central parts of

physiognomically and ecologically homogeneous vegetation stands. Within each of 315 sampling plots explored for snails, the snails were searched for by eye and collected in appropriate microhabitats for 1–2 h (for details: Horsák et al., 2015). For eight sites with a record of *Pupilla alluvionica* in the Altai Mountains (leg. M. Horsák, 2005-6, 2011), mean January and annual temperatures were obtained from the WorldClim database (Hijmans et al., 2005; www.worldclim.org) using the ArcGIS 8.3 program (www.esri.com). Elevation of these sites was measured with a GPS receiver (Garmin 60CSx) in the field.

To compare the general shell morphometry between fossil and modern samples, all adult and undamaged shells from the Pleistocene deposits and from two modern and abundant Altaian populations were measured and photographed. Shell measurements were conducted using an Olympus SZX9 microscope with the Infinity 2 Camera. Differences between modern and fossil populations in shell height and width were calculated using non-parametric Mann-Whitney U test. To compare shell measurements of *P. alluvionica* with its conchologically most similar species, *Pupilla muscorum* (Linnaeus, 1758) and *P. alpicola* Charpentier, 1837, we used already published data based on eight modern populations of *P. muscorum* and 22 populations of *P. alpicola* mostly from the Czech Republic and Slovakia, measured using the same methodology (for details: Horsák et al., 2010b).

## RESULTS AND DISCUSSION

Morphological comparison of shell measurements showed only small differences between the fossil samples described above and modern populations of *P. alluvionica* collected in the Altai Mountains (Table 1, Fig. 2). There were no consistent differences between the modern Altaian and fossil European populations in shell height. While no significant difference between fossil populations and the modern population from the Inua site (Mann-Whitney U test,  $P = 0.842$ ) was found, the shell height of the second modern population from the Kurai site was significantly higher (M-W U test,  $P < 0.001$ ) and for two fossil samples (i.e., Červený kopec K3 and especially Krems; Fig. 3) significantly smaller compared to the other populations. However, some shells from Červený kopec reached the maximum size of modern shells,



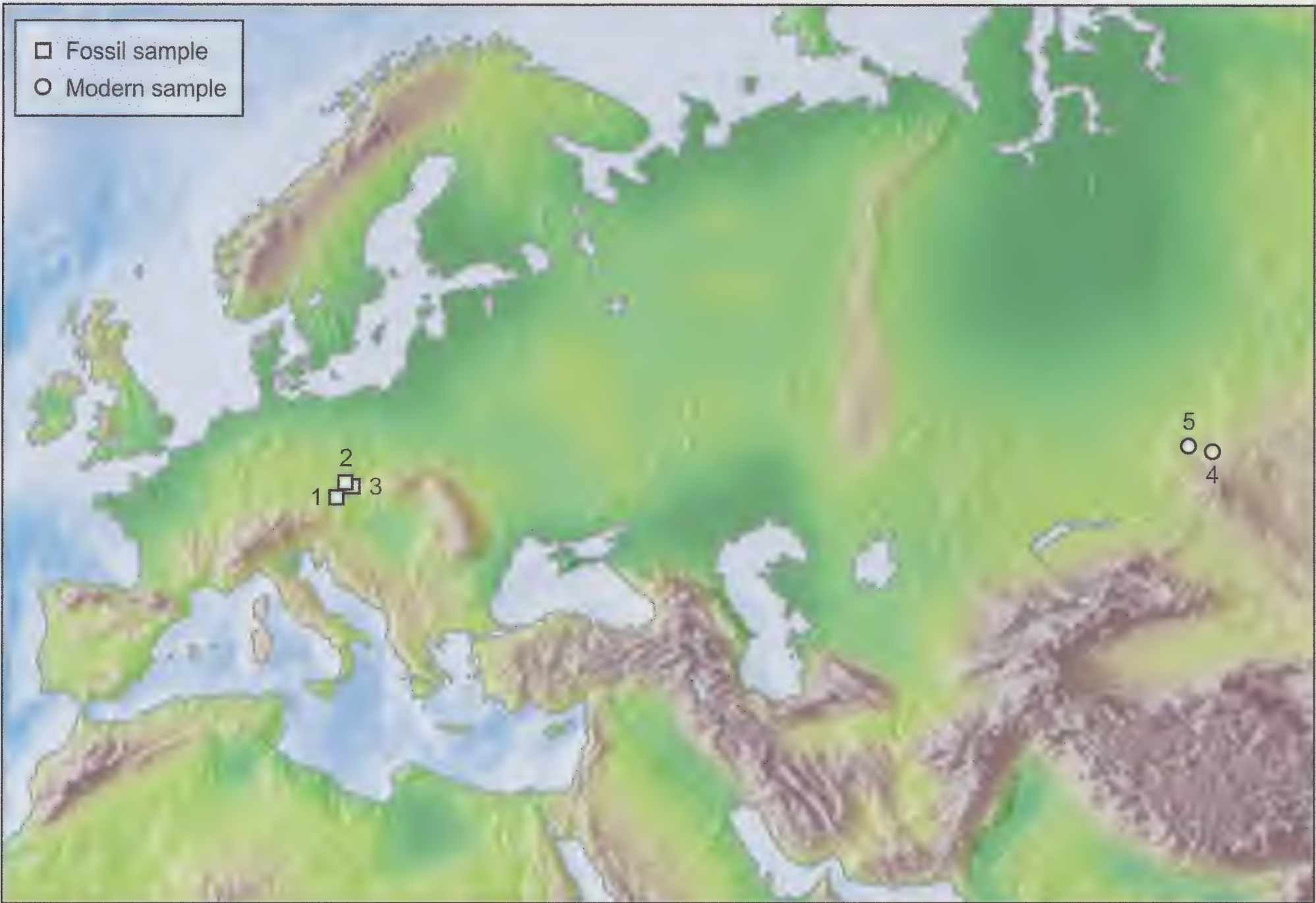


FIG. 1. Map of the studied fossil and modern samples (1: Krems an der Donau; 2: Brno, Červený kopec; 3: Brno, Stránská skála; 4: Altai, Kurai; 5: Altai, Inya). Base map: Mountain High Maps ©.

TABLE 1. Minimum, median and maximum values of shell height and width of *Pupilla alluvionica* based on nine Early-Middle Pleistocene samples (Krems an der Donau, Austria – five samples combined; three samples from Červený kopec and one from Stránská skála loess sites near Brno, Czech Republic), two modern populations from Russian Altai Mountains (limestone outcrops near Kurai and Inya settlements), and a combined data for *Pupilla muscorum* based on eight and for *P. alpicola* based on 22 modern European populations mostly from the Czech Republic and Slovakia (data adopted from Horsák et al., 2010b).

|                                        | N   | Shell height (mm) |        |      | Shell width (mm) |        |      |
|----------------------------------------|-----|-------------------|--------|------|------------------|--------|------|
|                                        |     | Min               | Median | Max  | Min              | Median | Max  |
| <i>P. alluvionica</i>                  |     |                   |        |      |                  |        |      |
| Krems (combined)                       | 5   | 3.66              | 3.83   | 3.85 | 1.95             | 2.04   | 2.05 |
| Stránská skála 11                      | 10  | 3.42              | 3.90   | 4.42 | 1.95             | 2.14   | 2.20 |
| Červený kopec K3                       | 18  | 3.54              | 3.76   | 4.20 | 2.04             | 2.13   | 2.22 |
| Červený kopec K4-1                     | 32  | 3.72              | 3.99   | 4.33 | 1.99             | 2.15   | 2.28 |
| Červený kopec K4-2                     | 20  | 3.69              | 4.06   | 4.30 | 2.04             | 2.15   | 2.20 |
| Kurai, Altai Mountains                 | 51  | 3.71              | 4.15   | 4.44 | 2.20             | 2.29   | 2.39 |
| Inya, Altai Mountains                  | 38  | 3.57              | 3.90   | 4.29 | 2.07             | 2.19   | 2.30 |
| <i>P. muscorum</i>                     |     |                   |        |      |                  |        |      |
| <i>P. alpicola</i> "typical"           | 206 | 2.65              | 3.20   | 3.70 | 1.65             | 1.70   | 1.80 |
| <i>P. alpicola</i> f. <i>pratensis</i> | 259 | 3.00              | 3.40   | 3.75 | 1.75             | 1.90   | 2.00 |
|                                        | 127 | 3.25              | 3.65   | 4.25 | 1.75             | 1.95   | 2.10 |



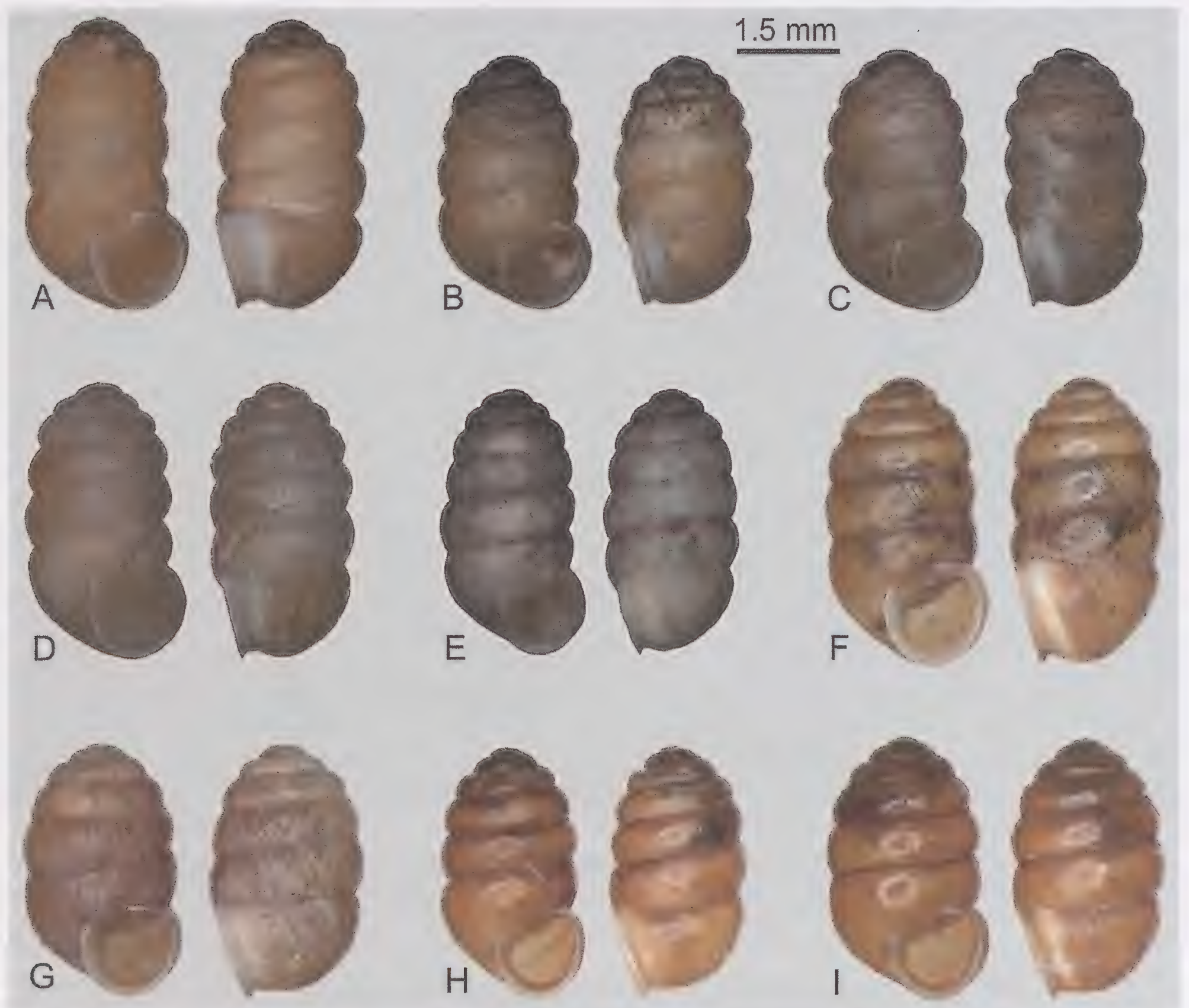


FIG. 2. *Pupilla alluvionica* fossil from Central European Early-Middle Pleistocene deposits (A–E) and modern from Russian Altai Mountains (F–I). Fossil: FIGS. A, B: Stránská skála 11 (49°11'28.2"N, 16°40'31.9"E), Brno, Czech Republic (A: 4.29 : 2.37 mm, B: 3.72 : 2.21 mm); FIGS. C, D: Červený kopec K4-2 (49°10'34.4"N, 16°35'10.6"E), Brno, Czech Republic (C: 3.86 : 2.25 mm, D: 4.07 : 2.23 mm); FIG. E: Krems an der Donau 65, (48°25'00.3"N, 15°35'49.2"E), Austria (3.85 : 1.95 mm); FIGS. F–G: Kurai (50°09'51.6"N, 87°48'31.1"E), Altai Mountains, Russia (F: 3.98 : 2.34, G: 3.73 : 2.23 mm); FIGS. H–I: Inya (50°24'05.0"N, 87°40'31.4"E), Altai Mountains, Russia (H: 3.69 : 2.12 mm, I: 3.87 : 2.31 mm). Photos by M. Horsák.

and no significant difference was observed between the Kurai and Červený kopec K4-2 sample (M-W U test,  $P = 0.136$ ). In contrast to shell height, shell width was significantly higher in modern shells (M-W U test,  $P < 0.001$ , Fig. 3), especially for the Kurai population (Table 1). However, median shell width of modern populations was only about 0.12 mm greater than that of any fossil sample except for the Krems material, where the shells were notably smaller in their width (Fig. 3). Comparison based on the other conchological characters confirmed that it is very likely that the examined Early-Middle Pleistocene fossil samples represent

the same species, *P. alluvionica*, still living in southern Siberian refugium of glacial fauna (Horsák et al., 2010a; Pavelková Řičáková et al., 2014).

The species is distinguished from all other Holarctic *Pupilla* species by its notably larger size (Nekola et al., 2015). On the basis of its other conchological characters (i.e., shell shape, surface structure, suture, and mouth barriers), it most closely resembles *Pupilla muscorum*, but its size is much larger, typically about 0.5 mm in shell height (Table 1). Another conchologically similar candidate is *Pupilla alpicola*, especially its form *pratensis*



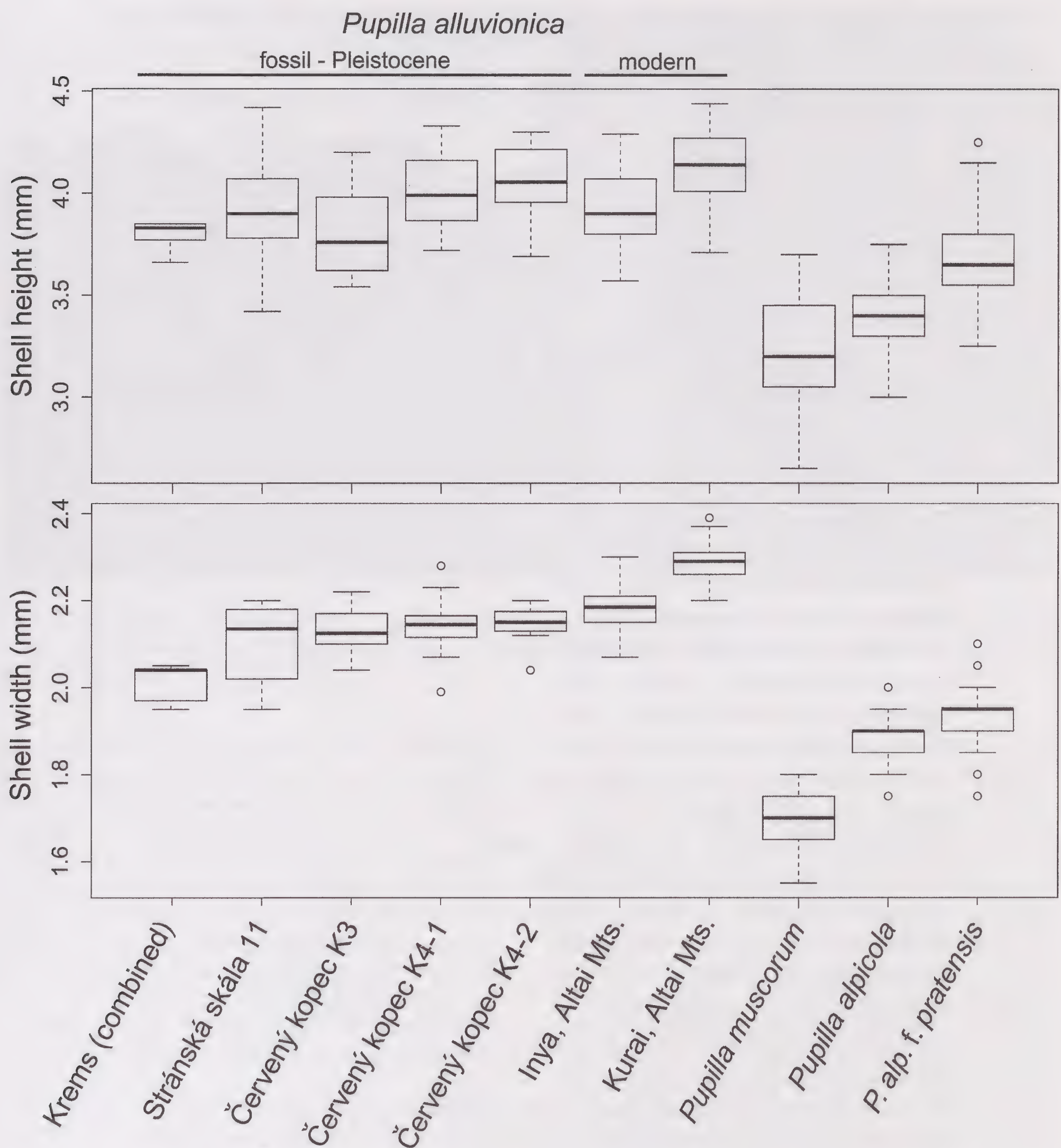


FIG. 3. Variation in shell height and width among nine studied fossil and two modern samples of *Pupilla alluvionica* and several modern populations of *P. muscorum* and *P. alpicola* (including formerly distinguished form *pratensis*). Note that five samples from Krems an der Donau were combined in one box as they contained a single shell each. For more details see Table 1. The central line of each box refers to the median value, box height to the interquartile range, whiskers to the non-outlier range (i.e., 1.5 times the interquartile range at each side), and small circles to outliers.

(Clessin, 1871), which is on average a bit bigger than a typical *P. alpicola* (Table 1; Horsák et al., 2010b). This species also has some similarities in shell characters, but with the exception of shells from Krems, all fossil samples overlapped neither in shell height nor in width with *P. alpicola* (Fig. 3). In this case, where conchological characters are inadequate, we

note that the ecological requirements of *P. alpicola* are radically different from those of *P. alluvionica*; the former occupies wetlands and the latter dry steppe, and the two species have never been found together (Meng & Hoffmann, 2008; M. Horsák, unpubl. data, Table 2). In the fossil faunas in Central Europe in which *P. alluvionica* was identified (Table 2), xerophile



TABLE 2. Land snail species and number of their records found in fossil (n = 9) and modern (n = 8) samples with *Pupilla alluvionica*.

| Species found with <i>P. alluvionica</i>             | No. sites |        |
|------------------------------------------------------|-----------|--------|
|                                                      | Fossil    | Modern |
| <i>Vallonia costata</i> (O. F. Müller, 1774)         | 6         | 8      |
| <i>Vallonia tenuilabris</i> (Al. Braun, 1842)        | 7         | 2      |
| <i>Pupilla turcmenica</i> (O. Boettger, 1889)        | ~         | 8      |
| <i>Pupilla triplicata</i> (Studer, 1820)             | 6         | 1      |
| <i>Clausilia dubia</i> Draparnaud, 1805              | 7         | ~      |
| <i>Fruticicola schrenkii</i> (Middendorff, 1851)     | ~         | 6      |
| <i>Helicopsis striata</i> (O. F. Müller, 1774)       | 6         | ~      |
| <i>Gastrocopta theeli</i> (Westerlund, 1877)         | ~         | 5      |
| <i>Granaria frumentum</i> (Draparnaud, 1801)         | 5         | ~      |
| <i>Nesovitrea hammonis</i> (Ström, 1765)             | 2         | 2      |
| <i>Euconulus fulvus</i> (O. F. Müller, 1774)         | ~         | 4      |
| <i>Cochlicopa lubrica</i> (O. F. Müller, 1774)       | 4         | ~      |
| <i>Gastrocopta serotina</i> Ložek, 1964              | 4         | ~      |
| <i>Quickella arenaria</i> (Potiez & Michaud, 1835)   | 4         | ~      |
| <i>Fruticicola fruticum</i> (O. F. Müller, 1774)     | 4         | ~      |
| <i>Vertigo parcedentata</i> (A. Braun, 1847)         | 4         | ~      |
| <i>Pupilla loessica</i> Ložek, 1954                  | 2         | 1      |
| <i>Truncatellina cylindrica</i> (Férussac, 1807)     | 2         | 1      |
| <i>Vertigo pusilla</i> O. F. Müller, 1774            | 3         | ~      |
| <i>Columella columella</i> (G. von Martens, 1830)    | 2         | ~      |
| <i>Euomphalia strigella</i> (Draparnaud, 1801)       | 2         | ~      |
| <i>Chilanodon bicallosa</i> (L. Pfeiffer, 1853)      | ~         | 2      |
| <i>Chondrula tridens</i> (O. F. Müller, 1774)        | 2         | ~      |
| <i>Pupilla sterrii</i> (Voith, 1840)                 | 2         | ~      |
| <i>Aegopinella minor</i> (Stabile, 1864)             | 1         | ~      |
| <i>Cochlicopa lubricella</i> (Rossmässler, 1835)     | ~         | 1      |
| <i>Discus ruderatus</i> (A. Férussac, 1821)          | 1         | ~      |
| <i>Isognomostoma isognomostomos</i> (Schröter, 1784) | 1         | ~      |
| <i>Macrogastrea plicatula</i> (Draparnaud, 1801)     | 1         | ~      |
| <i>Nesovitrea petronella</i> (L. Pfeiffer, 1853)     | ~         | 1      |
| <i>Punctum pygmaeum</i> (Draparnaud, 1805)           | 1         | ~      |
| <i>Succinella oblonga</i> (Draparnaud, 1801)         | 1         | ~      |
| <i>Trochulus sericeus</i> (Draparnaud, 1801)         | 1         | ~      |
| <i>Truncatellina claustralis</i> (Gredler, 1856)     | 1         | ~      |
| <i>Vallonia pulchella</i> (O. F. Müller, 1774)       | 1         | ~      |
| <i>Vallonia kamtschatica</i> Likharev, 1963          | ~         | 1      |
| <i>Vallonia ladacensis</i> (Nevill, 1878)            | ~         | 1      |
| <i>Vertigo</i> aff. <i>alpestris</i> Alder, 1838     | ~         | 1      |
| <i>Vertigo botanicorum</i> Horsák & Pokryzsko, 2010  | ~         | 1      |
| <i>Vertigo pygmaea</i> (Draparnaud, 1801)            | 1         | ~      |
| <i>Vertigo ronneyensis</i> (Westerlund, 1871)        | ~         | 1      |





FIG. 4. Limestone outcrops at the confluence of Chuya and Kurai rivers (Russian Altai Mountains) with a rich population of *Pupilla alluvionica* (left); the population used for the measurements. Photos by M. Horsák (left) and M. Chytrý (right).

species were very frequent (e.g., *Granaria frumentum*, *Helicopsis striata* and *Chondrula tridens*), but there were virtually no species exclusively confined to wetland environments. We note that this was true in all Krems samples in which *P. alluvionica* was identified (not shown). Although identification of some *Pupilla* species solely based on conchological characters can be doubtful (Nekola et al., 2015), we have only such characters to use; the distinctions are generally clear. Where they are not (Krems) the ecological data discounts any synonymy with *P. alpicola*.

We conclude that *Pupilla alluvionica* Meng & Hoffmann, 2008, is present both alive in the Altai and in Central European faunas from glacial periods earlier than ca. 0.8 mya. The eight modern populations sampled in the Altai Mountains were recorded in dry steppe or shrubby habitats, always associated with rocky limestone or chlorite schist outcrops (Fig. 4). These modern populations were mostly found in areas of rather warm climate at median elevation of 875 m a.s.l., with a median value of mean annual and January temperatures about 15.7°C and 1.6°C. However, the distribution of sites with the species varied between 280 and 2400 m a.s.l., defining also a rather wide range of macroclimatic conditions; from 3.2 to -3.8°C for mean annual temperature. Originally the species was reported from three

distinct locations (six populations) in the lower foothills of the central and eastern Russian Altai Mountains (Meng & Hoffmann, 2008). The species name “*alluvionica*” refers to the species occurrence in river alluviums, which was expected to be a characteristic habitat of this species. As we documented this species mostly from very dry steppe conditions (Fig. 4), far from any alluvial habitats, it seems that the species inhabits preferentially open habitats with sparse vegetation, but of variable humidity. It is also possible that those open active alluvia with coarse floodplain gravels where it was originally found by Meng & Hoffmann (2008) provide patches of relatively dry conditions for most of the year, which enable population growth once the species colonises these habitats from the surrounding habitats at rocky outcrops on slopes in valleys.

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## SPINE FORMATION AS A HATCHING TOOL IN *EUPRYMNA SCOLOPES* (MOLLUSCA, CEPHALOPODA, SEPIOLIDAE)

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### ABSTRACT

The hatching of an embryo from its egg is a crucial point in its development. This is the moment that decides whether the animal will be able to emerge and survive or whether it will remain trapped and die. Cephalopods usually produce enzymes in a system of glands known as the Hoyle organ, which weakens the chorion and enables hatching. In addition to this chemical approach, four cephalopod genera develop a terminal spine to further support the hatching process.

The presence of such a spine has been mentioned for the well-known cephalopod species *Euprymna scolopes*. However, little is known about either its structure or its cellular details. Our present results indicate that the spine consists purely of musculature, and no intermediate connective tissue was observed. No nerves were detected within the spine, although nerve fibers are present within the surrounding epithelium and dermal muscle layer, indicating that the spine stretching is controlled by this dermal musculature.

Our data show that the spine of *Euprymna* is similar in its composition to those of the other three cephalopod genera in which a spine has evolved. However, we found morphological differences in the spine tip and in a collagenous layer located between the spine and the normal epithelium. It remains unclear why two completely different but synergetic systems for hatching, the glandular Hoyle organ and a spine, exist in some, but not all, cephalopod genera.

Key words: Hoyle organ, hatching gland, embryonic development, spine formation, embryo, microCT, ultrastructure.

### INTRODUCTION

In cephalopods, hatching is effected by muscular mantle contractions or by enzymes released from a hatching gland known as the Hoyle organ (Orelli, 1959). This glandular system is present exclusively in the posterior part of the dorsal mantle surface and appears only during organogenesis (e.g., in *Sepia* from stage 22–23 onwards, and in *Loligo gahi* from stage 24–25 onwards; staging after Naef (1928)) (Orelli, 1959; Fioroni, 1962; Arnold & Singley, 1989; Cyran et al., 2013). In all decapod species, the Hoyle organ is shaped like an anchor, while in octopods it forms a slender horizontal band (Cyran et al., 2013). Enzymes

produced in the hatching gland weaken the cohesion of the chorionic membrane and enable the embryo to hatch.

In *Euprymna*, the Hoyle organ (HO) consists of one dorsal and two lateral bands, all slightly elevated (Fig. 1A). This enzymatic gland is formed during late embryonic development (at stage 25), is fully developed shortly before hatching, and disappears approximately two days after hatching (Cyran et al., 2013). Only one glandular cell type is present in the HO (Fig. 1B), which is distributed throughout the three bands. These cells are column-shaped, their nucleus is located basally and surrounded by several layers of rough endoplasmatic reticulum (rER) (not shown). At stage 26/27, the cells start

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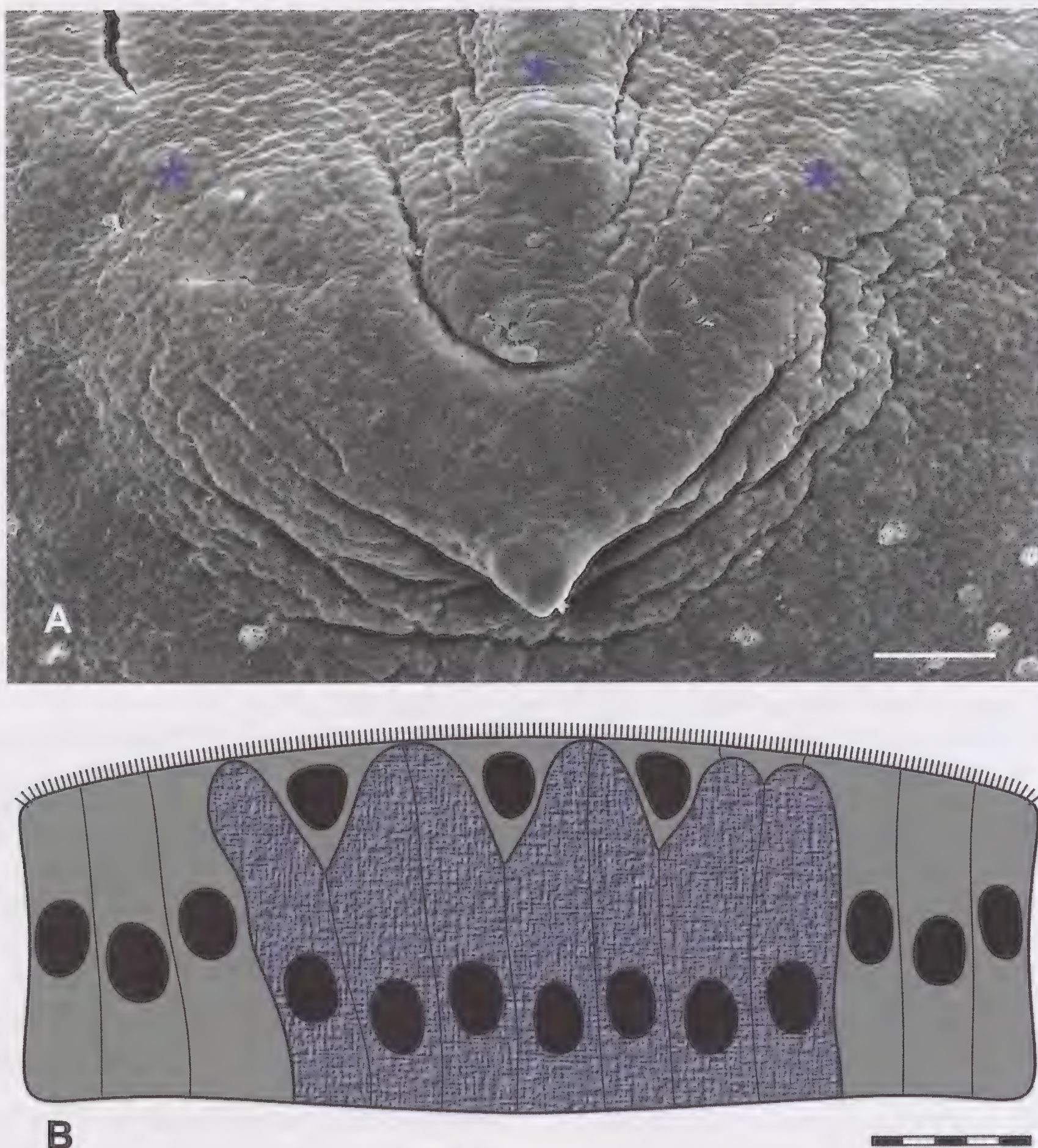


FIG. 1. (A): Scanning electron micrograph of the Hoyle organ in *Euprymna scolopes*, which appears at around stage 25 and forms one dorsal and two lateral bands that are slightly elevated (indicated with blue asterisks in the figure); (B): Schematic drawing of a cross section of the hatching gland showing that only one secretory cell type is present; the cells synthesize globular granules that are distributed evenly within the cells. Scale bar A, B = 50  $\mu$ m. Image B republished with permission from Cyran et al. (2013).

to synthesize spherical granules ( $\varnothing$  2–3  $\mu$ m) of uniform density. These granules are evenly distributed within the cells and show no signs of an increase in density towards the apical pole. The secretion of the granules takes place from stage 28 onwards (Cyran et al., 2013). Each cell excretes the most apical granules, while the residual cell content remains within the cells (Fig. 1B). As in all epithelial tissues of *Euprymna scolopes*, non-secretory cells are present in between the glandular cells (Cyran

et al., 2013). Within the HO, this cell type is triangular in section and located in the uppermost third of the epithelium layer; no connection to the basal lamina has been observed. The cells have a layer of short microvilli (0.4  $\mu$ m) on their apical surface and there are distinct cytoskeletal elements equally distributed within the cells of the HO as well as in the normal, neighboring epithelium (Fig. 1B) (Cyran et al., 2013).

In addition to the enzymatic hatching mechanism, some cephalopod species use additional



physical devices to hatch through the tough protective egg coats. In particular, four genera (namely *Sepiola*, *Sepietta*, *Rondeletiola* and *Rossia*) are mentioned as possessing a terminal, muscular spine near the hatching gland (Naef, 1928; Boletzky, 1991). Contrary to an earlier observation (Arnold et al., 1972), a terminal spine also occurs in *Euprymna* during the late embryonic phase, in addition to the Hoyle organ (Lee et al., 2009; Cyran et al., 2013).

Observations have shown that the embryos actively use both hatching tools; in *Euprymna*, in addition to the observed active synthesis and release of glandular material from the Hoyle organ (Cyran et al., 2013), the embryo pushes against the chorion with the spine to decisively facilitate the hatching process (Cyran et al., 2013), as in other sepiolids (Boletzky, 1991). Similar to the Hoyle organ, the spine also degenerates after hatching, however at a much slower rate than the hatching gland (Boletzky, 1991; Cyran et al., 2013).

Although the origin and morphology of the spine in some Sepiolidae species has been well documented, in this study we aim to shed further light on the spine morphology of *Euprymna scolopes* Berry, 1913, using ultrastructural and immunocytochemical data. Our results will contribute to the knowledge of the spine structure and muscular compositions, earlier mentioned by Boletzky (1991), and, in turn, comprehensively evaluate hatching strategies and “tools” in cephalopods.

## MATERIALS AND METHODS

Several specimens of *Euprymna scolopes* at different embryonic and post-hatching stages (stage 25 up to two-day-old hatchlings) were collected at the Paiko Peninsula, Oahu, Hawaii. The samples were fixed in 2.5% glutaraldehyde in a 0.1 M sodium-cacodylate buffer (pH 7.4, plus 10% sucrose) for 6 h at 25°C. All samples were subsequently immersed for 1.5 h in 1% osmium tetroxide with a 0.1 M buffer solution and dehydrated in a graded ethanol series. For transmission electron microscopy (TEM), the samples were embedded in Epon; ultrathin sections (50–70 nm) were mounted on copper slot grids, coated with formvar in dioxane, contrasted with uranyl acetate and lead citrate (Reynolds, 1963), and examined in a Zeiss EM 902 and Zeiss Libra 120. For scanning electron microscopy (SEM), the

samples were washed several times in 100% acetone, dried in a critical point dryer Leica CPD 300, mounted on stubs, coated with gold in a Polaron 5800 sputter coater, and viewed in the SEM Jeol IT 300.

For micro X-ray computed tomography ( $\mu$ CT), the glutaraldehyde-fixed samples were washed in demineralised water and dehydrated in a graded series of ethanol. Subsequently, the samples were contrasted for 36 h in 1% (w/v) phosphotungstic acid (PTA) in EtOH and transferred to water for scanning. The animals were imaged at high resolutions (1  $\mu$ m voxel size) using an Xradia MicroXCT 200 system.

For immunocytochemistry, the samples were fixed in a solution containing 4% PFA (Paraformaldehyde) in PBS (phosphate buffered saline) for 2 h at 25°C and subsequently washed three times in PBS. Immunocytochemical analyses of nuclei, muscles and nerve fibers were carried out on 100  $\mu$ m thick sections, cut with a vibratome (Leica VT 1200S). The sections were incubated with 2.5% Alexa Fluor TRITC-conjugated phalloidin (Invitrogen Carlsbad, California R415) and DAPI (D21490 Invitrogen Carlsbad, California) as well as 1:100 diluted acetylated  $\alpha$ -tubulin (Sigma-Aldrich St. Louis, MO T-6793 with FITC-labeled secondary antibody M308012 Invitrogen Carlsbad, California) (protocol: Wollesen et al., 2009, 2010).

## RESULTS

In this study, we observed that *Euprymna scolopes* develops a prominent spine on the posterior mantle pole during late embryonic development (Fig. 2A–C), beneath the merging bands of the HO. The spine first appears at stage 25 and grows continuously until hatching (stage 30). At hatching, the spine is conical in shape and around 100  $\mu$ m in length (Fig. 3A). After hatching, when the HO starts to disappear, the spine is still present, although it is not as prominent as prior to hatching (Fig. 2B, C). Unfortunately, we were not able to document the degradation of the spine during further early juvenile development as the animals died two days after hatching.

The spine arises from the connective tissue layer and is composed of numerous intersecting muscle fibers, which form a circle around its tapered tip (Fig. 4A). Nuclei are interspersed throughout the muscle system, while no intermediate connective tissue could be observed



in the spine tip area using electron microscopy (Fig. 3B). In the proximal area of the spine, the muscle bundles are more loosely arranged and merge with the dermal connective tissue (Fig. 3B), while toward the tip area the muscular arrangement becomes increasingly dense. The muscle system present in the spine and in the dermal epithelium appears distinct from the underlying mantle muscle, that is, they do not merge with each other. The tip itself stains strongly positive for phalloidin, showing a massive muscular compactness (Fig. 4B). Nerve fibers could be detected neither in the spine structure nor along the muscle fibers, but a loosely arranged network of nerve fibers is present in the surrounding epithelium and the dermal muscle layer (Fig. 4B). An approximately 1  $\mu\text{m}$  thick collagen layer (Fig. 3B) delimits

the spine from the normal mantle epithelium. This collagen layer could only be observed in the spine area, but neither in the normal epithelium nor in the HO. In the adult stages, the collagen layer is no longer present.

During early embryonic development, the spine is completely covered by the epithelium. In the late embryonic stages approaching the hatching phase, however, we observed signs of destroyed epithelial cells around the spine tip (Fig. 3C) and, furthermore, the spine itself appeared blunt in freshly hatched individuals (Fig. 2B, C).

It is not clear whether the destruction of the epithelial cells is caused by the final growth of the spine or occurs due to action of the embryo pushing with the spine against the chorion to penetrate the membrane.



FIG. 2. (A): Projection images of microcomputer tomographic image stacks of the *Euprymna* spine at stage 26. Due to the attached chorion and resulting spatial limitation, the spine is still folded. The bands of the Hoyle organ (indicated with blue asterisks in the figure) are clearly elevated and partly cover the spine; (B): Posterior; (C): Lateral view of a hatched specimen (about one day after hatching). The spine is shortened and appears blunt, which was likely caused by the chorion and jelly layer penetration during the hatching process. In addition, the bands of the Hoyle organ appear less prominent in comparison to the stage 26 specimen. Approximate scale bar A, C = 500  $\mu\text{m}$ .



## CONCLUSION

The present study confirms that, in addition to several other genera of the family Sepioliidae (*Sepiola*, *Rondeletiola*, *Sepietta*, *Rossia*) (Naef, 1928; Boletzky, 1991), *Euprymna scolopes* also possesses a terminal spine as a hatching device, parallel to the Hoyle organ. Unfortunately, to the best of our knowledge, it is not yet known whether embryos of other species in the subfamilies Rossiinae and Heteroteuthinae also form a terminal spine.

The only *Heteroteuthis* embryo known so far (Boletzky, 1978) was not sufficiently far advanced in development to provide an answer, and the available planktonic juvenile stages do not show clear traces of a terminal spine.

Similar to the spines described in the aforementioned sepiolid genera, the *Euprymna* spine is also conical in shape and located at the posterior mantle end beneath the Hoyle organ (Boletzky, 1991 and present study). The spine in *Euprymna* is, likewise, made of muscle tissue; however, with respect to its density, this spine more closely resembles the loose muscle bundle layers of *Sepiola* than the compact spine tissue of *Rossia* (Boletzky, 1991 and present study).

However, in contrast to the earlier general description by Boletzky (1986) for the Sepioliidae, the spine in *Euprymna* is not anchored to the mantle musculature, but clearly separated from it. Also, the *Euprymna* spine possesses a muscular compactness at its tip, which was not described previously (Boletzky, 1991). This morphological structure presumably supports and protects the spine during chorion penetration. The dermal neural network observed close to the spines of all genera (Boletzky, 1991 and present study) raises the question whether this hatching structure is contractile by itself or is just extended by the contraction of the mantle musculature.

According to Lee et al. (2009), the "terminal spine is extended by spine muscle contractions and mechanically perforates the chorion" in *Euprymna*. Since we were unable to detect nerves in the spine musculature, we could not confirm this hypothesis. Moreover, we were unable to observe any spine movements or contractions in *Euprymna* due to its small size and transparency as well as the opacity of the jelly layers covering the chorion. However, Cyran et al. (2013) confirmed the observation made by Lee et al. (2009) that the *Euprymna* embryo actively pushes and rubs its Hoyle

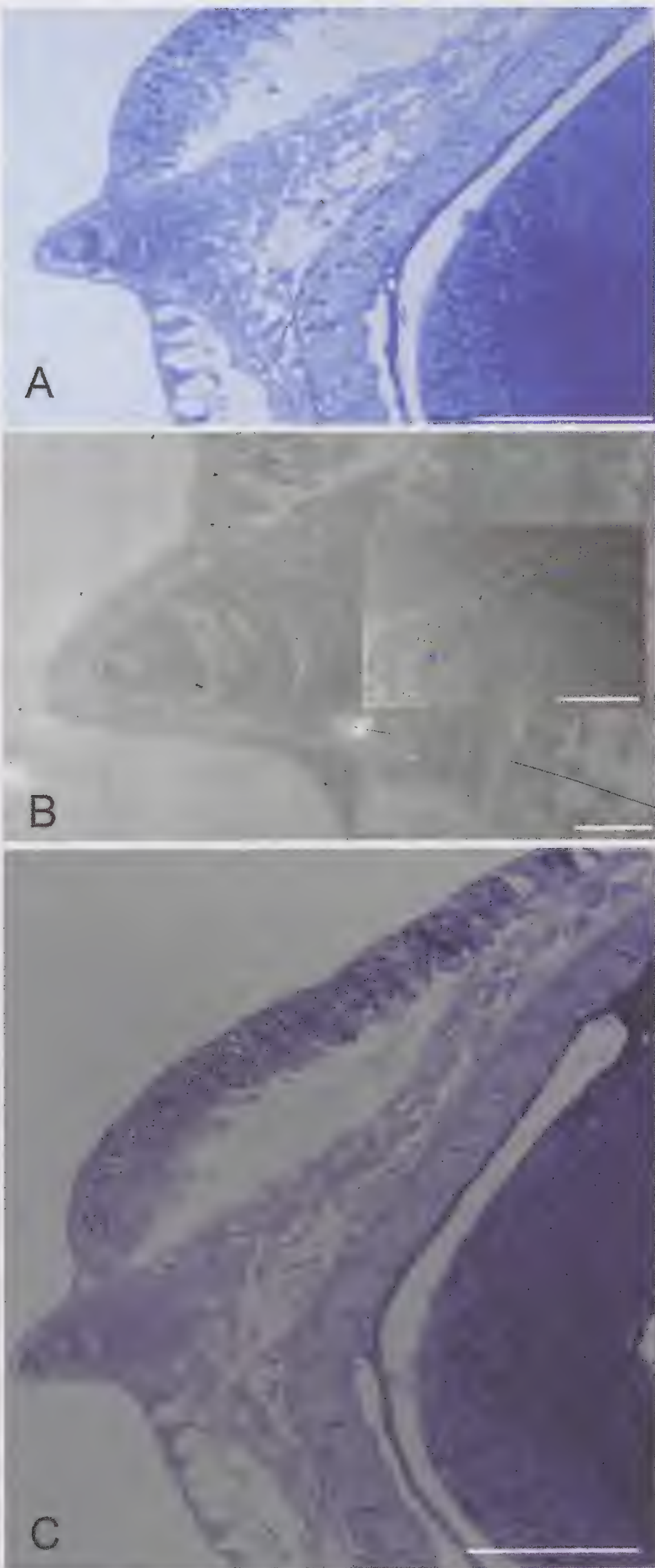


FIG. 3. (A): Semi-thin (1  $\mu$ m) section of the embryo at stage 30: The spine with its cone-like shape is clearly distinct from the surrounding normal epithelium; (B): Higher TEM magnification shows that a collagen layer is present between the normal mantle epithelium and the spine structure; the figure inset shows the collagen layer (blue arrowheads) at higher magnification. This layer is restricted to the spine area; (C): Semi-thin (1  $\mu$ m) section of the embryo after hatching (stage 1D) with the partially destroyed epithelial layer covering the spine. Scale bars in A, C = 100  $\mu$ m; B = 20  $\mu$ m; insert = 5  $\mu$ m.



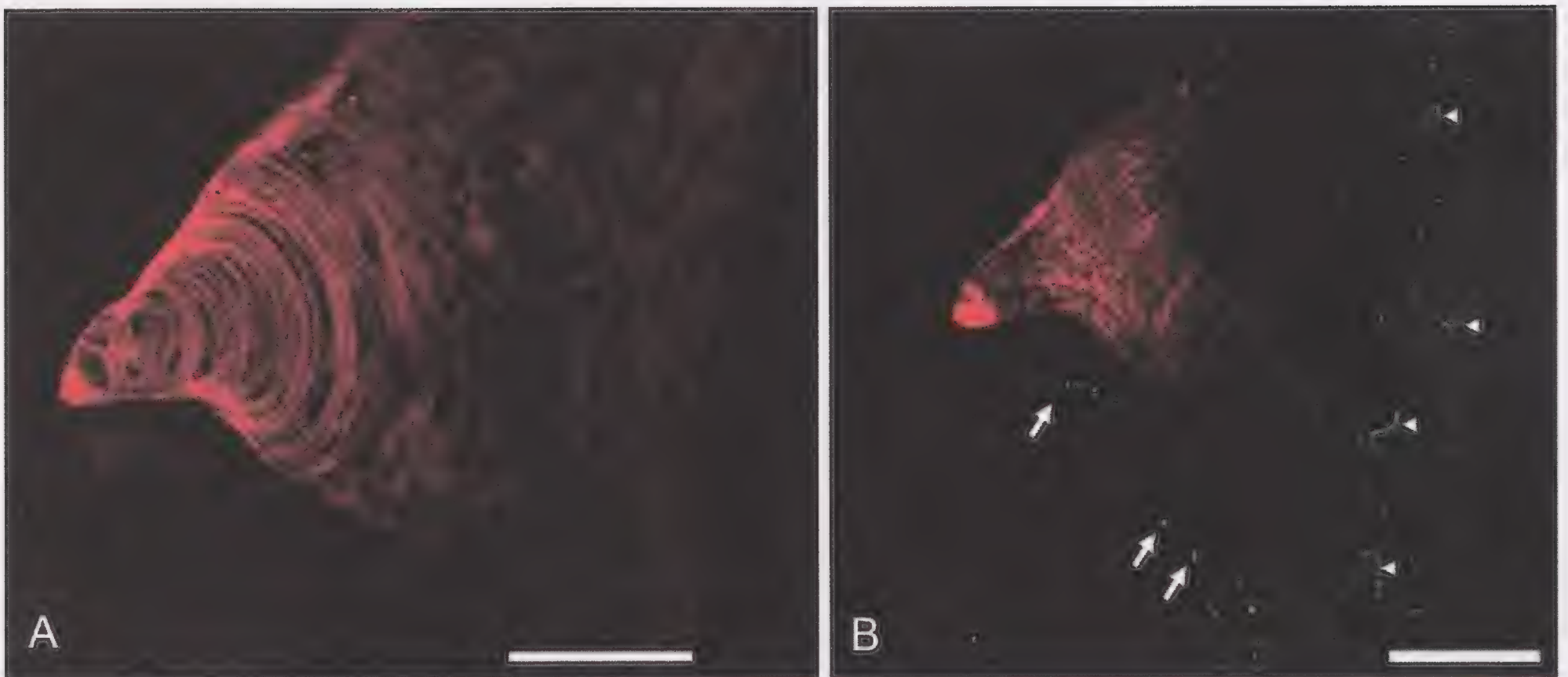


FIG. 4. Immunocytochemical images showing that the spine is composed of (A): Concentric muscle bundles (red staining, phalloidin labelling) which end in a massive muscular cap; (B): Nerve fibers (green,  $\alpha$ -tubulin antibody) could not be observed in the spine itself, but a loose network of nerves is present in the surrounding epithelium (arrow) and dermal muscle layer (arrow head). Scale bars A, B = 50  $\mu$ m.

organ and its terminal spine directly against the chorion during the hatching phase.

The collagen layer between epithelium and spine may serve as a mechanical damper. Since previous descriptions of the sepiolid spine did not mention a collagen layer (Boletzky, 1991), it remains unclear whether it was simply not detected or whether it indeed constitutes a specificity of *Euprymna scolopes*. Unfortunately, we could not verify the type of collagen (I, II or III) present in the *Euprymna scolopes* embryo. Appropriate tests with ubiquitous vertebrate antibodies (protocol: Lindenmair et al., 2014) have failed so far (data not shown), and need further investigation. Therefore, not only the muscular compactness at the spine tip, but also this layer are special formations in *Euprymna scolopes*, which may indicate a slightly different way of performing the same function in the hatching process as in the other genera.

Earlier observations showed that the spine in *Rossia* “degenerates only very slowly during juvenile development” (Boletzky, 1991), whereby spine remnants are still visible three months after hatching. In contrast, in *Sepietta* “it soon disappears after hatching” (Boletzky, 1991), while nothing is mentioned for *Sepiolo*. It remains unclear when the spine degeneration is complete in *Euprymna*, as the structure is still visible two days after hatching. However, since the spine is not documented in the adult

stage (Arnold et al., 1972; Klinger et al., 2010), we assume that the spine degrades during early juvenile development. Further investigations may be necessary to verify whether the species of the subfamily Sepiolinae (genera *Sepiolo*, *Sepietta*, *Euprymna*, as well as *Inio-teuthis*) have a shorter degeneration time than those of the subfamily Rossiinae.

An interesting question, which remains to be solved, is why these genera (*Sepiolo*, *Sepietta*, *Euprymna* and *Rossia*), all of them belonging to the family Sepiolidae, evolved two completely different but synergetic systems, namely the glandular Hoyle organ with its enzymatic substances and the spine for mechanical puncturing, in order to penetrate the egg layers during hatching. In the case of *Euprymna* it is known that the eggs are enclosed by several vitellin layers, which are very sticky and covered with sand for camouflage (Lee et al., 2009; Cyran et al., 2013). Although the thickness of the vitellin layers decreases during development until stage 30, the embryos are still tightly enclosed in the egg capsule and are not able to swim around freely as, for instance, the embryos of the pygmy squid *Idiosepius* can (Cyran et al., 2013). The embryo may therefore not be able to disperse the enzymes from the Hoyle organ along the chorion membrane as observed for other cephalopods (Cyran et al., 2013). Such a tight enclosure within the egg capsule is also described for *Rossia* (Boletzky, 1986), it could



therefore be assumed that this immobilization within the egg capsule is a major point for the spine formation.

From a systematical standpoint, the detection of the terminal spine in *Euprymna* embryos is in agreement with its position in the Sepiolidae. This family is presently subdivided into three subfamilies, namely Sepiolinae, Rossiinae and Heteroteuthinae (indeed the situation is more complex due to the occurrence of some incertae sedis genera and the somewhat unsatisfactory state of the Heteroteuthinae) (Boletzky, 1986; Young, 2007). The Rossiinae are believed to have a basal position with respect to the Sepiolinae, which are a fairly compact taxon within the Sepiolidae (Nishiguchi et al., 2004; Young, 2007); in agreement with this, the Rossiinae arose earlier than the Sepiolinae (Young et al., 1998). Hence, one can safely suppose that the terminal spine evolved first in *Rossia* (and/or in other rossiines) and, afterwards, this characteristic was inherited by the rossiine derived Sepiolinae. The fact that the spine persists for at least two days after hatching (present results), longer than in *Sepietta* (Boletzky, 1991), that is to say the spine persistence is alike or closer to *Rossia* than to *Sepietta*, is in good agreement with the basal position of *Euprymna* within the Sepiolinae (Nishiguchi et al., 2004; Bello, 1998). In order to have a comprehensive picture of both the evolutionary history of the terminal spine and its unique role in the Sepiolidae, albeit with finely graded specificity, investigations should be carried out in other taxa of the family: the sepioline genus *Inioteuthis*, other Rossiinae genera and, more compellingly, the Heteroteuthinae.

The terminal spine occurs exclusively in some sepiolid hatchlings, while other cephalopods use different tools to support the hatching phase. In decapods it is presumed that the integument ciliation supports "locomotion when the animal crosses the egg jellies" (Boletzky, 1982), while in incirrate hatchlings special integument structures (the K  lliker organs) act as hatching tools (Fioroni, 1981; Boletzky, 1982).

Further studies are necessary to uncover morphological and chemical differences in the composition of the chorion and perivitelline layers in different cephalopods. This will help to shed light on the role and need of a hatching tool in some cephalopod genera.

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## VARIATION IN THE SEX RATIO OF APPLE SNAILS (*POMACEA* SPP.) IN THEIR NATIVE RANGE

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### ABSTRACT

The brood sex ratio of the apple snail *Pomacea canaliculata* is highly variable among parents in areas where it has been introduced. Such variation in the sex ratio may reflect variation in the source population, or it may have stemmed from the mixture of multiple source populations with different sex-determining mechanisms. To distinguish these hypotheses, the sex ratios of  $F_1$  (hatchlings from wild-collected egg masses) and  $F_2$  snails (produced from crosses of the  $F_1$  snails) from three sites in the native range in Argentina were studied. The sex ratios of the  $F_1$  snails were not significantly different from 0.5, although there was a slight but significant difference among populations. The  $F_2$  broods from intra-population crosses also lacked variation in the sex ratio. However, the sex ratios in  $F_2$  broods from inter-population crosses were highly variable, from 0 (all females) to 0.84 (mostly males). Thus, the large variation in the sex ratio in areas where *P. canaliculata* has been introduced is probably due to the mixture of source populations.

Key words: Ampullariidae, Argentina, Caenogastropoda, polygenes, sex determination, sex-ratio bias.

### INTRODUCTION

The sex ratio is one of the most fundamental reproductive characteristics in sexual organisms (Fisher, 1930; Charnov, 1982; Bull, 1983; West, 2009). In most cases, the sex ratio within a population is 0.5 (proportion of males), because of frequency-dependent selection that stabilizes an equal number of males and females (Fisher's theory; Fisher, 1930). As long as this 0.5 population sex ratio is guaranteed, parents that produce any sex ratio are equally adaptive if the population is large enough (Verner, 1965). However, in small populations, parents that produce offspring with a sex ratio that differs significantly from 0.5 will have lower fitness than those producing offspring with a 0.5 sex ratio (Verner, 1965; Williams, 1979). Therefore, large variation in the sex ratio of offspring in small populations is enigmatic.

There are several examples of large sex ratio variation in small populations in animals (Bull, 1983). There are three major, non-mutually exclusive mechanisms that may cause such large sex ratio variation. First, even under a simple genetic sex determination mechanism

(e.g., XY or ZW), parents may control the sex ratio of offspring in an adaptive way according to the environment (Trivers & Willard, 1973), which has been studied mainly in vertebrates and insects (West, 2009). Second, the sex ratio will vary according to the environment if sex determination is influenced environmentally, as observed in many invertebrates (Bull, 1983; West, 2009; Beukeboom & Perrin, 2014). Third, if sex is determined by a combination of multiple genes (e.g., X, Y, and Z sex chromosomes in lemmings; Bull, 1983; Bachtrog et al., 2014), the sex ratio of broods will vary according to the genotypes of the parents; such variation due to polygenic sex determination is observed in copepods (Alexander et al., 2014), polychaetes (Premoli et al., 1996), and fishes (Liew et al., 2012).

Among molluscs, large sex ratio variation has been relatively well documented in mussels (*Mytilus*: Saavedra et al., 1997; Yusa et al., 2013; Zouros, 2013) and apple snails (*Pomacea*: Yusa, 2007a; Hayes et al., 2015). The mechanism underlying sex ratio variation has been studied in the apple snail *Pomacea canaliculata*, partly in the hope of developing a control method for this highly invasive

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species and important agricultural pest (Joshi & Sebastian, 2006; Hayes et al., 2015). In areas where it has been introduced, large variation has been reported among broods, yet the population sex ratio is close to 0.5 in at least two populations in Kumamoto (Yusa & Suzuki, 2003) and one population in Nara, Japan (Kumagai & Yusa, pers. obs.). No environmental effects are known (Yusa, 2004), and the variation appears to be controlled by a small number of nuclear genes (Yusa, 2006, 2007a, b). Because density of overwintered snails is very low after cold winters (average 0.15 snails m<sup>-2</sup> in Nara; Yoshida et al., 2009), the effective population size can be fairly small in some areas and the diverse brood sex ratios do not appear to be adaptive there.

One possible cause of putative polygenic sex determination is that it stems from a mixture of multiple source populations with different sex-determining mechanisms. For instance, if one population has a sex-determining locus with X and Y alleles and another has a different locus with Z and W alleles, the merged population might have complicated sex determination with two loci and four sex-determining alleles. In animals, differences in sex-determining mechanisms among populations are known in several taxa (Bachtrog et al., 2014; Beukeboom & Perrin, 2014), including a frog (Ogata et al., 2003), fish (Shinomiya et al., 2004; Roberts et al., 2009), and the housefly (Hamm et al., 2015).

The merging of multiple populations is likely for apple snails, because genetic evidence strongly suggests that several strains of *P. canaliculata*, and of a related species, *P. maculata*, have been introduced in Asia (Hayes et al., 2008), and the two species appear to have hybridized in several places (Matsukura et al., 2013). If mixing of populations (or even species) with different sex-determining systems is the cause of large variation in the sex ratio in apple snails in areas where they have been introduced, we would expect the sex ratio to be less variable in native populations. If so, we predict that crosses between individuals from the same population will lead to unbiased sex ratios, whereas crosses between individuals from different populations will lead to biased sex ratios. However, artificial introduction appears to occur even in their native South America (Martín et al., 2001), and Matsukura et al. (2013) found genetic evidence for hybridization in some South American populations. Thus, we might also find variation in the sex

ratio in some native populations. The goal of this study was to distinguish between these two possibilities, namely whether the variation in the sex ratio also exists in areas where the species is native or whether it stems from the mixing of multiple source populations with different sex-determining mechanisms. We tested these predictions using three native populations of *P. canaliculata* in Argentina.

## MATERIALS AND METHODS

### Collection of Egg Masses

Egg masses, rather than adult or juvenile snails, were collected because egg masses of *Pomacea* snails are laid above the water in ponds and swamps and are therefore easier to collect in large numbers. They were collected from three sites in Argentina: (1) San Miguel de Tucumán, Catalinas Park (T population; 26°49'S, 65°13'W); (2) Santa Fe de la Vera Cruz, South Park (F population; 31°38'S, 60°42'W); and (3) San Nicolás de los Arroyos, Regional Forest and Botanical Park "Rafael de Aguiar" (N population; 33°20'S, 60°13'W). More than 20 egg masses per site were collected in November 2010 and were imported to Japan before hatching. The T and F populations correspond to the A1 and A4 populations, respectively, in Matsukura et al. (2013). The T population was therein identified to be *P. canaliculata* by the sequence of mitochondrial COI and the nuclear EF1 $\alpha$  genes. In the present study, most F<sub>1</sub> and F<sub>2</sub> individuals of the T population also had the pure *canaliculata* genotypes (shown as the "CC" type in Tables 1–3). However, one F<sub>2</sub> individual used for an inter-population cross had *maculata*-type COI and *canaliculata*-type EF1 $\alpha$  (the "MC" male in TxN-1, indicating the source population of the father, that of the mother, and the pair identity in this order; Table 3). The F population contained individuals with *maculata*-type COI and *canaliculata*-type EF1 $\alpha$  in Matsukura et al. (2013) and most individuals also had this genotype in this study (the "MC" type in Tables 1–3), suggesting that hybridization had occurred in this population. Likewise, F<sub>1</sub> and F<sub>2</sub> snails from the N population were sequenced, and they included pure *canaliculata*-type individuals as well as mixture of *maculata*- and *canaliculata*-types (the "CB" or "MB" types), suggesting past hybridization events also in this population.



Sex Ratio of the F<sub>1</sub> Generation (Experiment 1)

Each egg mass was allowed to hatch in a petri dish at 25°C with 14:10 h photoperiods. When the hatchlings appeared, six were randomly selected from each of the 20 egg masses per population (N = 120) and reared together in a 22.5 L aquarium with aeration. Initially, the water depth was set to 2 cm, before being increased to 10 cm as the hatchlings grew. Commercial food pellets for carp (Hikari mini pet, Kyorin, Hyogo, Japan) were added as required, and a small amount of powdered oyster shell was occasionally added as a calcium supply. The water was changed at least once a week.

Once the snails reached 14 mm in shell height (which took a minimum of 50 days), most were dissected and the sex was identified by the presence or absence of a testis (Yusa & Suzuki, 2003; Yusa, 2004). Seventy two snails were not dissected but served as the parents of the next (F<sub>2</sub>) generation. Their sex was initially determined by the presence or absence of a testis, as observed through the thin shell while alive (Yusa, 2007b) for pairing purposes and later confirmed by dissection. The sex ratio was defined as the proportion of males among the snails that survived to the final assessment of sex.

Sex Ratio of the F<sub>2</sub> Generation (Experiments 2 and 3)

Immature snails with a shell height of 14–18 mm, hatching from the field-collected egg masses (F<sub>1</sub> generation), were paired. For intra-population crosses (Experiment 2), six pairs of each of the T, F, and N populations were formed (N = 18 pairs in total). In addition, for inter-population crosses (Experiment 3), six pairs were formed for each of the combinations of TxF, FxN, and NxT populations (N =

18 pairs in total). The numbers of male and female parents were balanced (e.g., three T males were mated to three F females, and vice versa). Each pair was reared in a 1.5 L perforated container placed in a larger (60 L) container with water circulation under the same laboratory protocol as above.

The egg masses were checked almost daily, and the first or second viable egg mass from each pair was collected, kept in a petri dish, and allowed to hatch. Up to 40 hatchlings per egg mass were reared in a 1.0 L perforated container, placed in the 60 L container under the same conditions as the F<sub>1</sub> pairs, and then sexed.

Statistical Analyses

Generalized linear models with binomial errors and a logit link function were used as statistical analyses using JMP version 11 (SAS Institute, Cary, North Carolina). In each of the three experiments, population (or their combination in Experiment 3) and identity of the pair (nested within the population; included only if broods from more than one pair were available per population) were specified as explanatory variables, and the sex was specified as the response variable. In addition, binomial tests were conducted to show if the sex ratio of each brood was different from 0.5, and a Pearson’s correlation analysis was conducted to test if there was any relationship between the survival rate and the sex ratio caused by sex-biased mortality.

RESULTS

Sex Ratio of the F<sub>1</sub> Generation (Experiment 1)

The survival rate of hatchlings from field-collected egg masses (F<sub>1</sub> generation) during rearing was between 0.66 and 0.80 (Table 1). The

TABLE 1. Sex ratio of F<sub>1</sub> snails hatched from field-collected egg masses in three populations in Argentina.

| Population      | Male | Female | Sex Ratio | P (Binomial Test) | Survival Rate | Male Genotype* | Female Genotype* |
|-----------------|------|--------|-----------|-------------------|---------------|----------------|------------------|
| T (Tucuman)     | 35   | 49     | 0.42      | 0.16              | 0.70          | CC4            | CC3              |
| F (Santa Fe)    | 46   | 33     | 0.58      | 0.18              | 0.66          | CC1, MC3       | MC4              |
| N (San Nicolás) | 40   | 56     | 0.42      | 0.13              | 0.80          | CC1, CB1, MB1  | CC1, CB1         |

\*The first character denotes COI sequence, the second EF1α sequences, and the digit number of individuals sequenced. C = *canaliculata*-type, M = *maculata*-type, B = both types.



TABLE 2. Sex ratio of F<sub>2</sub> snails from intra-population crosses.

| Population | Pair | Male | Female | Sex Ratio | P (Binomial Test) | Survival Rate | Male Genotype* | Female Genotype* |
|------------|------|------|--------|-----------|-------------------|---------------|----------------|------------------|
| T          | 1    | 11   | 11     | 0.50      | 1.00              | 0.55          |                | CC               |
| F          | 1    | 8    | 10     | 0.44      | 0.81              | 0.45          | MC             | MC               |
| F          | 2    | 15   | 17     | 0.47      | 0.86              | 0.80          | MC             | MC               |
| N          | 1    | 15   | 17     | 0.47      | 0.86              | 0.91          | CC             | CC               |
| N          | 2    | 19   | 15     | 0.56      | 0.61              | 0.85          | CB             | MB               |
| N          | 3    | 13   | 25     | 0.34      | 0.07              | 0.95          | CB             |                  |
| N          | 4    | 12   | 24     | 0.33      | 0.07              | 0.90          | CC             | MC               |
| N          | 5    | 12   | 18     | 0.40      | 0.36              | 0.75          | CB             | CM               |

\*The first character denotes COI sequence, and the second EF1α sequences. C = *canaliculata*-type, M = *maculata*-type, B = both types. Blank cells indicate that the genotypes could not be determined.

sex ratio of hatchlings from the T population was 0.42 (35 males: 49 females), which was not significantly different from 0.5. Similarly, the sex ratios of F and N populations did not differ significantly from 0.5 (Table 1). However, the overall effect of population on the sex ratio was just significant (generalized linear model; likelihood  $\chi^2 = 6.06$ ,  $df = 2$ ,  $P = 0.048$ ).

Sex Ratio of the F<sub>2</sub> Population from Intra-population Crosses (Experiment 2)

Eight out of the 18 F<sub>2</sub> intra-population crosses resulted in the production of viable offspring (Table 2). The remaining pairs did not mate or lay egg masses, or, if they did, the eggs did not hatch.

The survival rate during rearing ranged from 0.45 to 0.95 (Table 2), although it had no significant relationship with the sex ratio ( $N = 8$ ,  $r$

$= -0.30$ ,  $P = 0.47$ ). The intra-population crosses resulted in sex ratios of 0.33–0.56, with some crosses within the N populations having the lowest (0.33, 0.34), but none differed significantly from 0.5. The generalized linear model also showed that the overall effects of population or pair identity on the sex ratio were not significant (population, likelihood  $\chi^2 = 0.64$ ,  $df = 2$ ,  $P = 0.73$ ; pair, likelihood  $\chi^2 = 5.13$ ,  $df = 5$ ,  $P = 0.40$ ).

Sex Ratio of the F<sub>2</sub> Population from Inter-population Crosses (Experiment 3)

Only four of the 18 F<sub>2</sub> inter-population crosses resulted in the production of offspring (Table 3). In particular, no mating was observed in many crosses, partly due to different timing of maturation (T snails matured within 1 year and became senescent whereas most F and N snails did not mature until the second year).

TABLE 3. Sex ratio of F<sub>2</sub> snails from inter-population crosses.

| Population* | Pair | Male | Female | Sex Ratio | P (Binomial Test) | Survival Rate | Male Genotype** | Female Genotype** |
|-------------|------|------|--------|-----------|-------------------|---------------|-----------------|-------------------|
| TxF         | 1    | 0    | 33     | 0         | < 0.001           | 0.83          | CC              | MC                |
| TxN         | 1    | 8    | 31     | 0.21      | < 0.001           | 0.98          | MC              | CB                |
| FxN         | 1    | 31   | 6      | 0.84      | < 0.001           | 0.93          | MC              | CM                |
| FxN         | 2    | 3    | 6      | 0.33      | 0.51              | 0.23          |                 |                   |

\* The first character denotes the father's population and the last the mother's.

\*\*The first character denotes COI sequence, and the second EF1α sequences. C = *canaliculata*-type, M = *maculata*-type, B = both types. Blank cells indicate that the genotypes could not be determined.



The survival rate during rearing ranged from 0.23 to 0.98 (Table 3), but it had no significant relationship to the sex ratio ( $N = 4$ ,  $r = 0.10$ ,  $P = 0.90$ ). In contrast to the intra-population crosses, all but one of the inter-population crosses resulted in highly biased sex ratios (Table 3). One cross (FxN-1) produced an offspring sex ratio significantly biased toward male offspring, and two crosses (TxF and TxN) were significantly biased toward female offspring. The remaining cross (FxN-2) resulted in a sex ratio slightly biased toward female offspring, but the tendency was not significant, probably because of the small number of offspring that survived to be sexed ( $N = 9$ ). The generalized linear model also showed that the effects of both population and pair identity on the sex ratio were significant (population, likelihood  $\chi^2 = 28.47$ ,  $df = 2$ ,  $P < 0.001$ ; pair, likelihood  $\chi^2 = 8.55$ ,  $df = 1$ ,  $P = 0.003$ ).

## DISCUSSION

In the  $F_2$  intra-population crosses (Experiment 2), the sex ratio was not significantly different from 0.5 in any brood. Thus, unlike in areas where it has been introduced, populations of *Pomacea* spp. in areas where the species are native generally appear to have unbiased brood sex ratios. Although only the averages are known because the snails were mass cultured, the sex ratios of the  $F_1$  population were also unbiased (Experiment 1).

In contrast, although the sample size is small, inter-population crosses (Experiment 3) generally resulted in much more biased sex ratios than did intra-population crosses and the large variation was similar to that in areas where the species have been introduced (Yusa & Suzuki, 2003). This indicates that crosses between genetically more distant individuals result in a bias in the sex ratio, supporting the hypothesis that variation in sex ratio in areas where the species have been introduced is mainly due to the mixture of different source populations.

However, the difference in the sex ratio among populations at the  $F_1$  generation (Experiment 1) was slight (ranging from 0.42 to 0.58) but significant ( $P = 0.048$ ). Therefore, the possibility that sex ratios are also biased in areas where the species are native cannot be ruled out. All the three populations contained both *P. canaliculata* and *P. maculata* genotypes (Matsukura et al., 2013; this study), indicating hybridization had occurred in these popula-

tions. This may be the reason for the slight inter-population difference of the sex ratio. However, even if hybridization had occurred, the native populations showed less variability in brood sex ratio than the introduced ones. Fisherian selection for an equal sex ratio (Fisher, 1930) might have occurred in such native populations over time.

A major confounding effect in this study is mortality before the assessment of sex. Sex-specific mortality may change the sex ratio at maturity, even if the birth sex ratio is 0.5 (Yusa, 2007a). We cannot test this possibility in the  $F_1$  generation because only three populations were studied, which is not enough to detect a significant relationship. However, such sex-specific mortality is unlikely to have affected the results of the  $F_2$  brood sex ratios because there was no significant relationship between the survival rate and the sex ratio in either intra-population or inter-population crosses. Likewise, many unsuccessful crosses among different populations made the number of replicates small. The major reasons of unsuccessful crosses were low hatchability of eggs from crosses between genetically distant strains (Matsukura et al., 2013) and the different timing of maturity among populations. It appears that T snails, which is nearly pure *P. canaliculata*, matured and became senescent earlier than N and F snails that have genes from *P. maculata*, a much larger species than *P. canaliculata*.

Still another complication is that all the three populations were of hybrid origins, which was unexpected when we started the experiments. Hybridization between two species sometimes results in sex ratio bias in the  $F_1$  generation (McDermott & Noor, 2010). This is partly because a species has often accumulated selfish genetic elements that divert sex ratios (e.g., meiotic drive genes) and their suppressors that revert the sex ratio to 0.5 (Orr & Irving, 2005; McDermott & Noor, 2010). Such sex ratio bias has been documented in crosses between two species of freshwater snails (*Viviparus ater* and *V. contectus*; Trüb & Ribi, 1997). In this study, hybridization between two species is not the immediate cause of observed sex ratio bias because our genetic analysis denied the possibility that we used two distinct species for crosses (Tables 1–3). In addition, our results differ from typical results of crosses between two species, in that (1) sex ratio is biased in both directions and (2) the bias is not explained by differential mortality between sexes. However, we cannot deny the possibility



that factors that affect sex ratios in this study originally stem from past hybridization events between *P. canaliculata* and *P. maculata*. Even so, our conclusion that the sex ratio bias is due to mixing of populations with different sex factors still holds. Anyway, crosses using pure *P. canaliculata* and *P. maculata* are needed to determine the origin of the factors responsible for the sex ratio bias.

In summary, the variation in the sex ratio of *P. canaliculata* in areas where it has been introduced is most likely due to the mixture of different source populations. However, the sex ratios in native populations were slightly biased from each other, possibly due to past hybridization events. In general, the variation in the sex ratio due to multiple genes tends to be unstable and converges to a simple sex-determining system fairly soon (Bull, 1983). If so, the occurrence of large amounts of variation in the sex ratio in introduced populations after > 30 years of introduction (Yusa & Wada, 1999) remains enigmatic. Further research is needed to determine the reason for the maintenance of the variation in sex ratio in areas where the species have been introduced, as well as the sex ratio in the pure native populations.

#### ACKNOWLEDGEMENTS

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OBSERVATIONS ON THE BIOLOGY AND SCLEROCHRONOLOGY  
OF “*TURRITELLA*” *DUPLICATA* (LINNAEUS, 1758)  
(CERITHIOIDEA, TURRITELLIDAE) FROM SOUTHERN THAILAND

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ABSTRACT

*Turritella duplicata* (Linnaeus, 1758) is a marine suspension-feeding gastropod found in shallow-marine and tidal flat environments throughout Southeast Asia and the Indo-West Pacific. It was studied on a tidal flat in the national park of Nopparat Thara in the district of Krabi, southern Thailand. *Turritella duplicata* was found primarily in the lower intertidal zone, and 90 specimens were gathered and measured. Their geographical positions on the flat were mapped, revealing zonations in population distribution, both parallel and perpendicular to the shore-line. The size distribution of the shells indicates that the population consists exclusively of adults.  $\delta^{18}\text{O}$  sclerochronology performed on three shells shows variations of up to 1.5‰ associated with seasonal changes in water parameters, suggesting longevity of about three years and seasonally controlled growth rates. The absence of juveniles and observed population distribution coupled with the sclerochronological data suggest that reproduction occurs in early spring, and that the population represents three cohorts approximately one year in age and older. Migration to deeper water during other seasons cannot be ruled out. Smaller individuals were preferentially found on the inner tidal flat, and individuals older than two years preferentially colonised the outer tidal flat. The carbon isotopic composition of the analysed shells partially tracks these life stages, suggesting that metabolic “vital effects” are influencing the  $\delta^{13}\text{C}$  of the shells.

Keywords: stable isotopes, sclerochronology, vital effects, tidal flat, scarring, breakage.

INTRODUCTION

Gastropods of the family Turritellidae, subfamily Turritellinae (*sensu* Marwick, 1957) are important components of many marine benthic communities (Allmon, 1988, 2011). Although turritellines occur in a variety of environments, they are most abundant in cool water and rare in tropical carbonate environments (Allmon, 1988, 2007). Little is known about the biology of Recent species, especially from tropical waters. This paper is part of a series of reports (Allmon et al., 1992, 1994; Waite & Allmon, 2013) that seek to remedy this situation. Here we summarize all available information on the biology of *Turritella duplicata* (Linnaeus, 1758), based on the literature and new observations of the species in southern Thailand.

*Turritella duplicata* were studied in their natural habitat on the tidal flat of Nopparat Thara beach, part of the National Park of Nopparat Thara in the district of Krabi, southern Thailand

(Fig. 1). The locality was chosen because it is a truly tropical occurrence and because personal communication with several experienced shell collectors had established the Nopparat Thara area as an easily accessible locality for finding large intact turritelline shells.

Despite their importance in many modern marine environments and extensive fossil record, the supraspecific systematics of turritellines remain poorly understood (Allmon, 1996, 2011; Beu, 2010). At least 40 genera or subgeneric names have been proposed within the subfamily Turritellinae, with at least another 15 in other subfamilies (Houbrick, 1988; Allmon, 2011). Most of these are inadequately defined and poorly studied (Allmon, 1996). It has long been widely accepted among systematists that the genus name *Turritella* Lamarck, 1799 (type species *T. terebra* (Linnaeus, 1758)), should not be applied to most of these species (Palmer, 1937; Marwick, 1957).

Linnaeus (1758) described *Turbo duplicatus*, *T. acutangulus* and *T. replicatus* as separate

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species. In 1799 Lamarck created the genus *Turritella*, and in 1822 he placed *Turbo duplicatus* Linnaeus in it as *Turritella duplicata*. In 1849 Reeve synonymised the three species of Linnaeus under *T. duplicata*, which has been followed by most modern authors (e.g., Garrard, 1972; but see Paul et al., 2013). In 1840, Gray had listed the generic name *Zaria*, but did not give a type species, and so as of that date the genus was a *nomen nudum* (Neave, 1940: 693). In 1847 (p. 155), however, Gray proposed *Turbo duplicatus* as the type species of *Zaria* making the genus available (Marwick, 1957: 164). (Bouchet & Rocroi (2005) incorrectly give Gray (1842) as the author of the genus.) Several authors in the past have used *Zaria* as a subgenus of *Turritella* (e.g., Tryon, 1883; Baluk, 1975, 2006; Beets, 1986).

Beu (2010) and Allmon (1996) point out that the generic-level systematics of the turritellines are, at best, inconsistent and problematic and that only molecular phylogeny studies will be able to resolve these inconsistencies. Here the trivial name *duplicata* is used in the sense of Reeve (1849), and the genus "*Turritella*" is used *sensu lato*, as has previously been done by Allmon (1996). The following synonymy/chresonymy lists the major systematic works and does not aim to be exhaustive.

## SYSTEMATICS

Family Turritellidae Lovén, 1847  
Subfamily Turritellinae Lovén, 1847  
Genus *Turritella* Lamarck, 1799

Type species: *Turbo terebra* Linnaeus, 1758.  
Recent, Indo-Pacific.

### *Turritella duplicata* (Linnaeus, 1758)

- 1758 *Turbo duplicatus* Linnaeus: 766.
- 1758 *Turbo acutangulus* Linnaeus: 766.
- 1758 *Turbo replicatus* Linnaeus: 766.
- 1822 *Turritella duplicata* (Linnaeus) – Lamarck, 1822: 56.
- 1843 *Turritella duplicata* "Lamarck" – Deshayes & Milne-Edwards, 1843: 251.
- 1847 *Zaria duplicata* (Linnaeus) – Gray, 1847: 155.
- 1849 *Turritella duplicata* (Linnaeus) – Reeve, 1849: 571, pl. 1, fig. 2.
- 1879 *Turritella duplicata* "Lamarck" – Martin, 1879: 69, pl. 11, fig. 13.
- 1883 *Turritella (Zaria) duplicata* (Linnaeus) – Tryon, 1883: 224, pl. 67, fig. 59.
- 1957 *Zaria duplicata* (Linnaeus) – Marwick, 1957: 165, figs. 40, 47.
- 2009 *Zaria duplicata* (Linnaeus) – Harzhauser et al., 2009: 343.

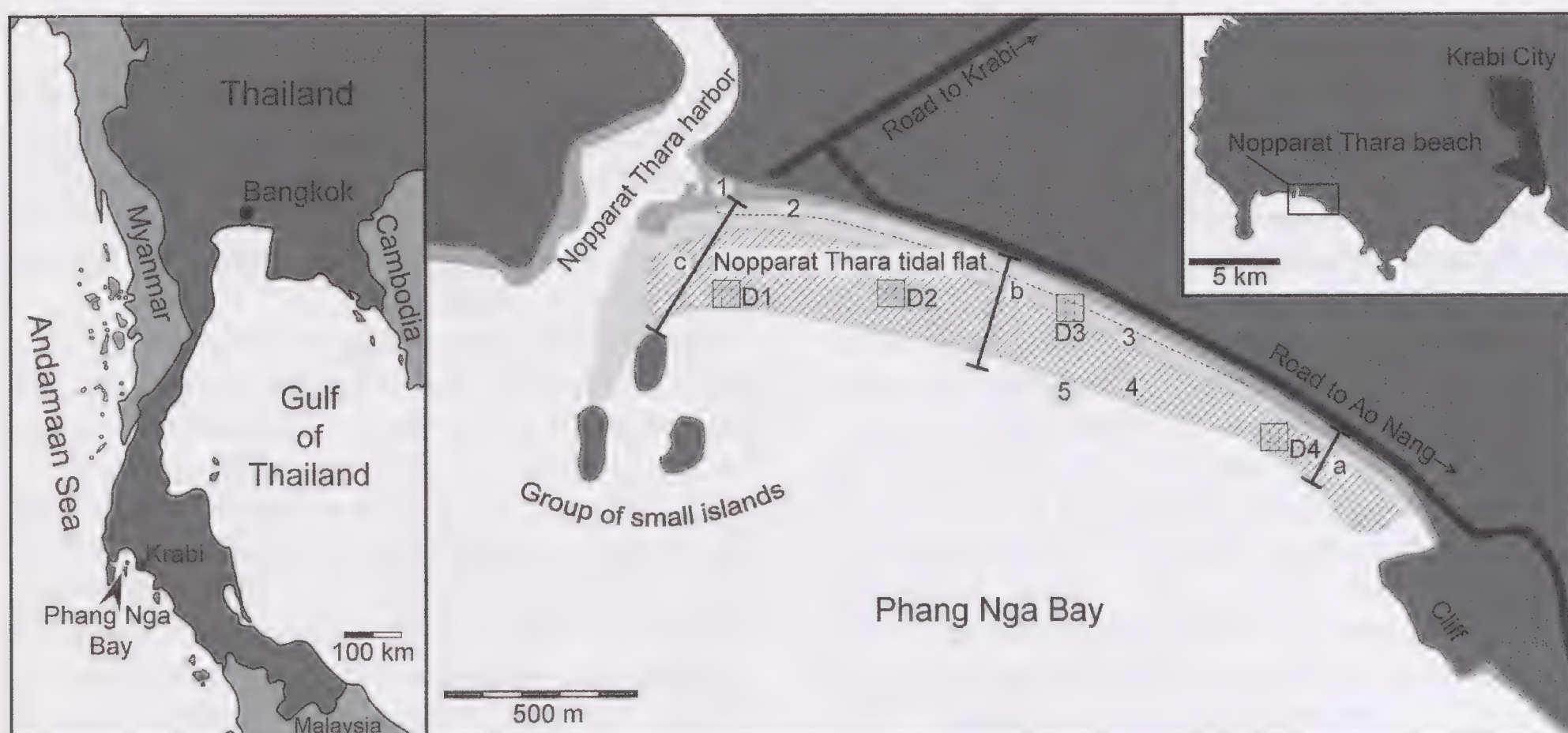


FIG. 1. Map of the study area depicting the Nopparat Thara tidal flat and its position on the Andaman Sea coast. (1) Beach, (2) Near shore or ocpode zone, (3) Intermediate zone, (4) Turritellid zone, (5) Firmground zone; a–c refer to the positions of the transects described in Fig. 3; D1–D4 refer to the positions of the excavations on the tidal flat (Modified from Waite & Strasser, 2011, p. 226, fig. 1, © Springer-Verlag 2010; with kind permission from Springer Science & Business Media B. V.).



## DESCRIPTION AND GEOGRAPHIC DISTRIBUTION

## Description

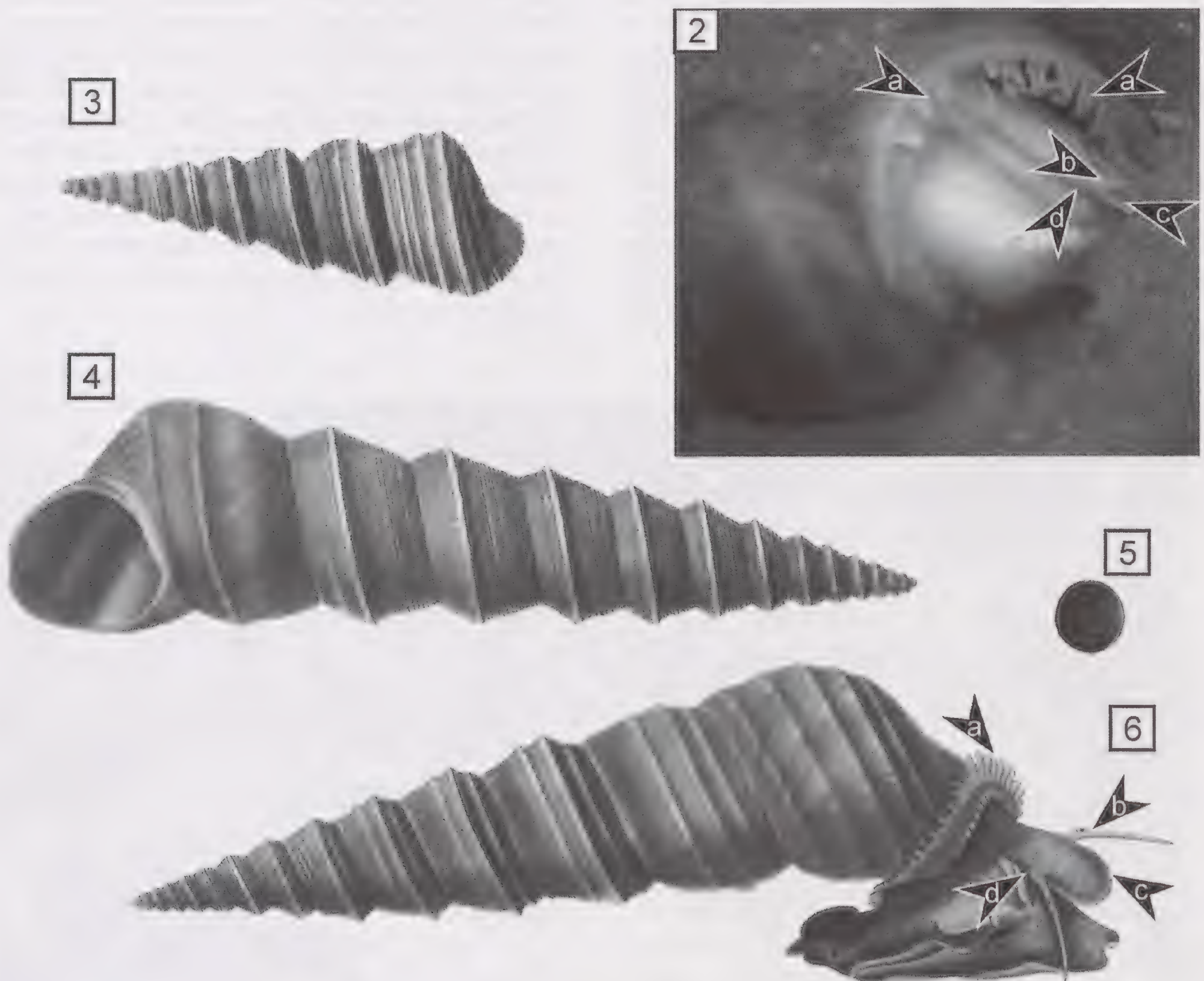
*Turritella duplicata*, the two-keeled screw shell, for full descriptions of the shell, see Reeve (1849) and Kiener (1873).

Shells can reach at least 160 mm in length and about 40 mm in basal diameter, with at least 25 whorls. Our observations on the soft part anatomy confirm the description provided by Allmon (2011: fig. 2), and the illustrations of Kiener (1873), reproduced here in Figs. 2–6. The head-foot has a short, wide snout, and a pair of long cephalic tentacles, each with

an eye situated near the base. The foot itself is relatively small, with a ciliated groove on the right side. The aperture is fringed by two rows of non-branching papillae or tentacles, which prevent the entrance of large particles. The operculum is small, permitting the animal to retreat into the shell far enough to vacate the lowest two whorls. Ratios between the diameters of opercula and the respective shell apertures range between 1.8 and 2.3.

## Geographic Distribution

Indo-West Pacific: from Madagascar to Indonesia; north to the Gujarat coast of India and the Philippines and south to northern



FIGS. 2–6. Anatomical features of *T. duplicata*. FIG. 2. Underwater photograph of *T. duplicata* burying itself. Visible elements of soft part anatomy include: a = outer rim of papillae, b = tentacle with eye, c = snout, d = food groove; FIGS. 3, 4: Sketches of shells of *T. duplicata* copied from Kiener (1873); FIG. 5: Sketch of the corresponding operculum to the specimen figured in Fig. 4; FIG. 6: Sketch of hard- and soft part anatomy of *T. duplicata*: a = outer rim of papillae, b = tentacle with eye, c = snout, d = food groove.



Queensland (Poutiers, 1998; Saravanakumar et al., 2007; Fig. 7). It is known to occur in intertidal waters but maximum depth range is unknown.

#### Temporal Distribution

It was reported from the Upper Miocene (Martin, 1879), where it was only known from one fossil locality on Java. According to Hoek Ostende et al. (2002), however, that is a misidentification. There is no other published fossil record.

#### Geographical and Geological Setting of the Nopparat Thara Tidal Flat

The Nopparat Thara beach is situated on the Phang Nga Bay coast and forms the extension of the Ao Nang beach. It lies west of Ao Nang in the district of Krabi, southern Thailand (Fig. 1). Along the Phang Nga coast, sand flats and mud flats alternate with steep cliffs, the mud flats predominantly facing east and the sand flats west. The region's climate is dominated by the reversing monsoon, which is responsible for a rainy season and south-westerly winds from April to October and a cooler dry season

with north-easterly winds from November until March. Rainfall averages around 300 mm/month in the wet season and 50 mm/month in the dry season. Sea surface temperatures range from 27–31°C and salinities are generally between 32 and 33‰ (Tudhope & Scofin, 1994).

The Nopparat Thara beach is separated from the Ao Nang beach by a small cliff that defines the eastern end of the studied tidal flat (Fig. 1). The western termination of the tidal flat is an estuary that drains a low-lying swamp area, and forms a busy harbour for long-tail and tourist boats. Tides are semi-diurnal and tidal range during the study period varied between about 3.2 m at spring tide to about 1.0 m at neap tide. Winds during the surveying period were weak, but consistently from the southeast. In the east, the beach is relatively narrow (~15 m wide) and the flat is steep, so during low tide a rather narrow expanse of tidal flat is exposed. The beach is narrowest in the central part and then broadens out towards the west. A sand-spit is formed at the estuary mouth due to long-shore currents and sediment transport (Fig. 1). Here, a broad expanse of the flat is exposed at low tide.

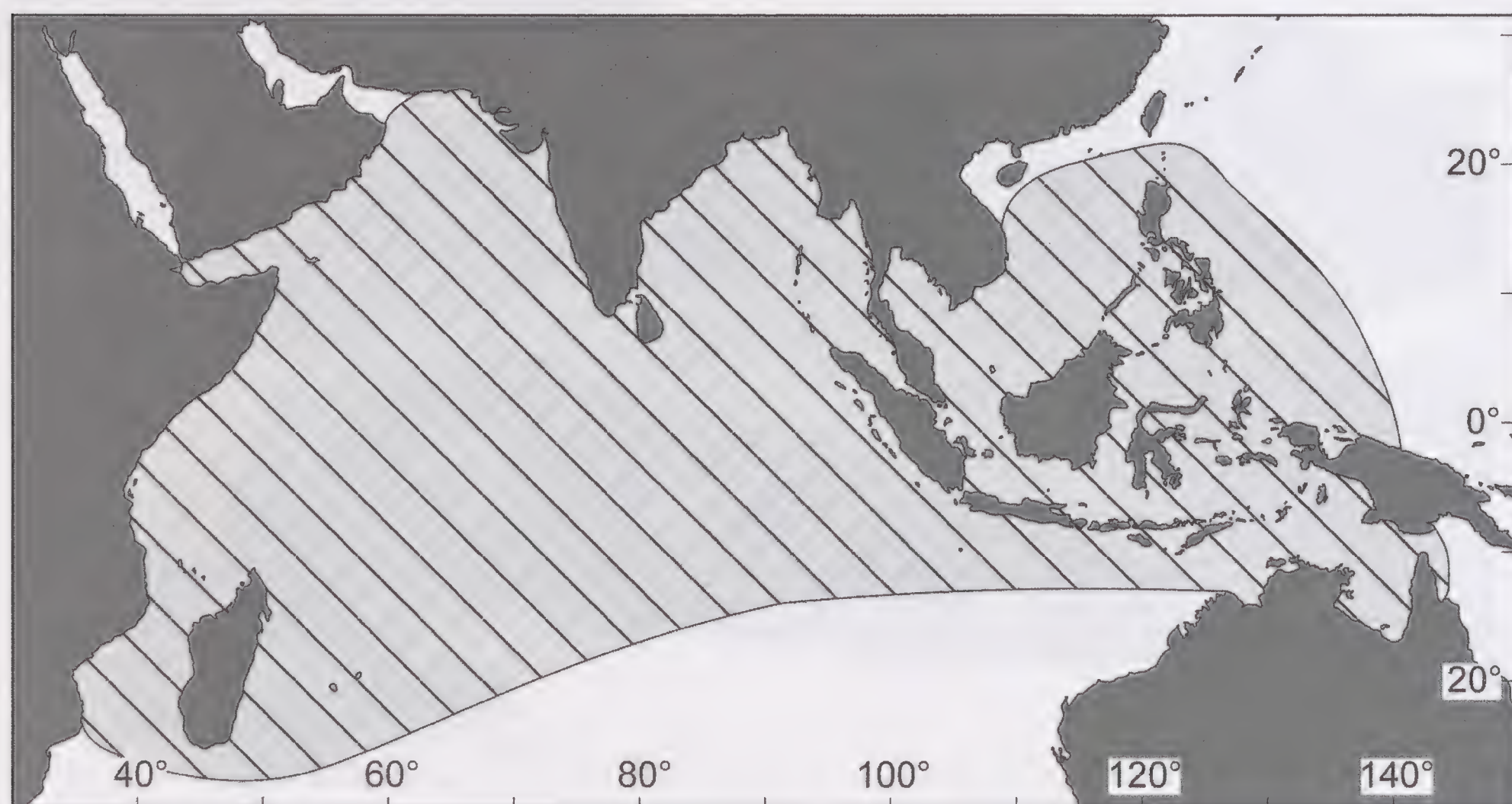


FIG. 7. Known distribution of *T. duplicata* (hatched area) modified from Poutiers (1998) (Caramagna, 1875; Sundaram et al., 1969; Purchon & Purchon, 1981; Rajagopal et al., 1990; Saravanakumar et al., 2007).



## MATERIAL AND METHODS

## Field Observations

During an eight-day (10.–17.02.2008) period the Nopparat Thara tidal flat and beach were monitored, focusing on the activity of turritelline gastropods both when accessible during low tide and during high tide by means of snorkelling. Systematic mapping was performed during daytime low tide periods by documenting transects parallel and perpendicular to the beach line. Transects were conducted on foot in straight lines from the beach to the low-tide water line, or from tidal channel to tidal channel respectively. Transects were replicated as well as possible during high-tide periods by snorkelling. Documented features included topography, sediment composition, sediment stability (due to algal/fungal overgrowth), and sediment water content, as well as benthic faunal elements. Four excavations over an area of 9 m<sup>2</sup> to a depth of 5 cm were conducted to document frequencies and variations of shallow infauna across the flat.

Representative measurements of water parameters (salinity, alkalinity, specific gravity, pH, Ca and Mg contents) were made with a SALIF-ERT test kit. Temperature measurements were made with a dive chronometer and visibility was estimated during snorkeling.

A total of 77 live and 13 well-preserved dead specimens of *T. duplicata* were collected from the beach and tidal flat. Specimens were measured in length and basal width and documented and catalogued with regard to their location and position on the flat or beach, their state of preservation and any unusual or interesting features. After examination, the live turritellines were returned to the field. Five well-preserved dead shell specimens were brought back to the lab. All shells were treated with 20% H<sub>2</sub>O<sub>2</sub> to remove organic remains.

## Isotope Sampling

In the absence of direct observations, indirect methods for estimating growth rates in molluscs can be applied. Seasonally controlled variations in the oxygen stable isotopic composition of shell carbonate can be analysed to determine growth rates in different species of modern and fossil turritellines (Allmon et al., 1992, 1994; Jones & Allmon, 1995; Waite & Allmon, 2013). The same technique was used on three shells of *T. duplicata* in the present

study. All of the analysed specimens were collected dead from the Nopparat Thara tidal flat.

Specimen *Td1* was found at the sediment surface during snorkelling under permanent cover of water in the vicinity of the islands, although it was in pristine condition it is unclear how long it had already been dead. Specimens *Td2* and *Td3* were both found on the flat during low tide and were so recently dead that part of the decomposing animal and the opercula were still inside the shell. The first two specimens were approximately the same size, being (*Td1*: 19 whorls, complete aperture, 4 uppermost whorls of teleoconch missing) 145 mm and (*Td2*: 19 whorls, complete aperture, 5 uppermost whorls missing) 144 mm respectively in length. The third specimen was slightly smaller with a total length of (*Td3*: 19 whorls 2 uppermost whorls missing) 115 mm. The sampling yielded 79 separate drilled powder samples (*Td1*: 31, *Td2*: 21, *Td3*: 17). In *Td1* the uppermost 2–3 whorls were combined to one sample whereas in *Td2* and *Td3* the uppermost whorls were not sampled. In *Td1* and *Td2* two samples were extracted from the lowermost 4 whorls and in *Td3* from the lowermost two whorls. One sample was extracted from each of the remaining whorls.

For the preparation of aragonite powder samples for isotope analysis, shell surfaces were cleaned with hydrochloric acid and rinsed with distilled water and alcohol. Isotope samples were extracted manually with a dental drill.

## Isotope Analysis

About 400 µg of powdered sample were flushed with helium (120 ml/min for 5 min) and then reacted with 100% phosphoric acid offline for 24 hrs at 50°C before analysis, based on the method of McCrea (1950). All samples were analysed for their carbon- and oxygen-isotopic composition at the Cornell Isotope Laboratory (COIL) at Cornell University. The C- and O-isotope composition was measured using a Thermo Scientific Delta V isotope ratio mass spectrometer (IRMS) interfaced to a Thermo Finnigan Gas Bench II, in continuous flow mode using He carrier gas. The method used four measuring peaks for each sample. Average values of the samples measured were normalized using two international standards and checked with an internal standard. The overall standard deviation for the internal

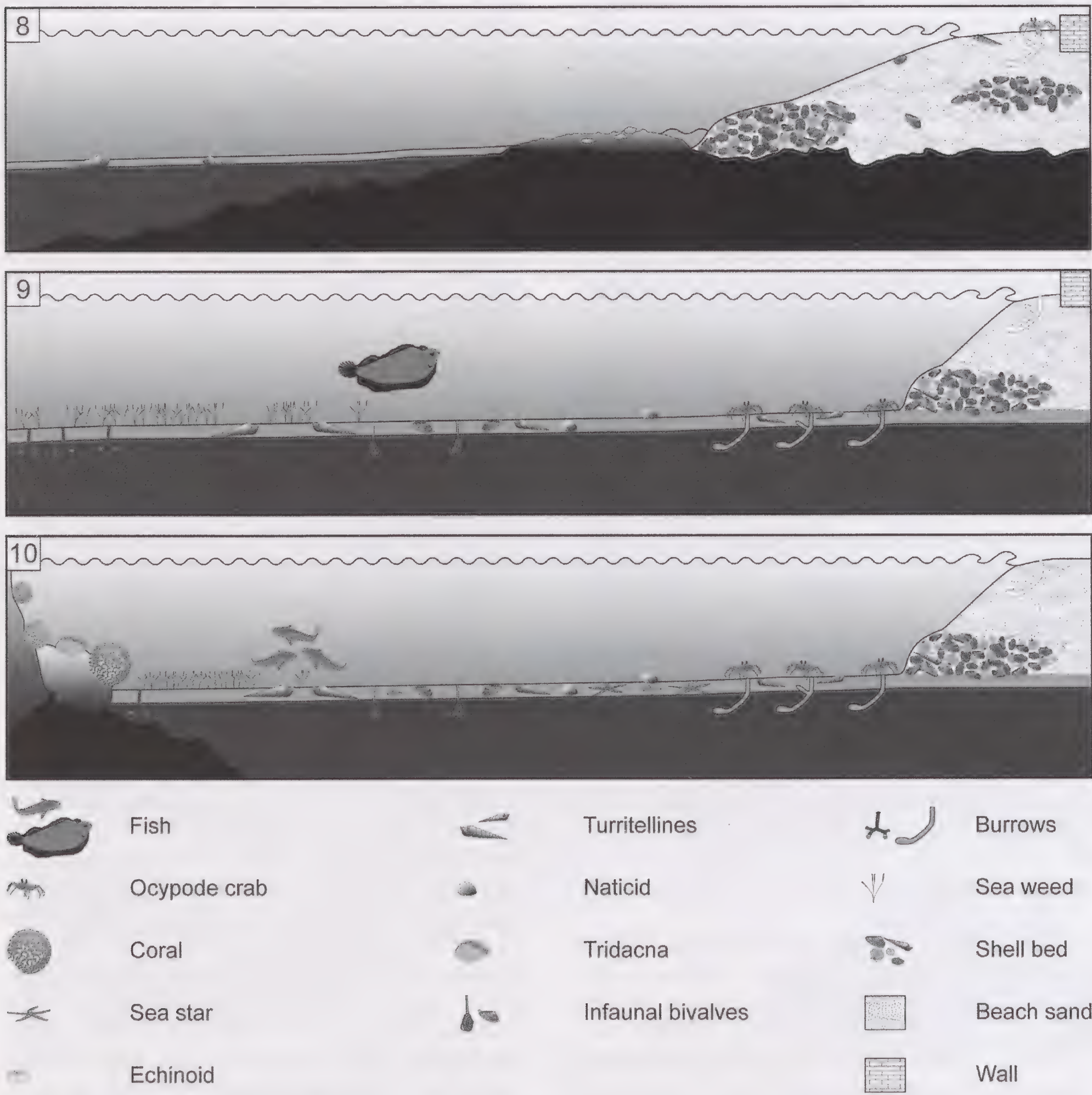


carbonate standard was 0.31‰ for  $\delta^{13}\text{C}$  and 0.11‰ for  $\delta^{18}\text{O}$ . Isotope corrections are performed using a two-point normalization based on internationally calibrated standards (NBS 18 and NBS 19). Values have not been corrected for any differences between the calcite and aragonite acid fractionation factors; for all samples only the acid fractionation factor for calcite has been used. Isotope compositions are expressed in notation as per mil deviations from the international VPDB carbonate standard.

Figured Specimens

The figured specimens are stored at the Paleontological Research Institution in Ithaca, New York. Collection numbers for isotope voucher material are as follows:

- Td(1) NPt PRI 68215: *Turritella duplicata* shell from Nopharat Thara, Krabi, Thailand
- Td(2) NPt PRI 68216: *Turritella duplicata* shell from Nopharat Thara, Krabi, Thailand
- Td(3) NPt PRI 68217: *Turritella duplicata* shell from Nopharat Thara, Krabi, Thailand



FIGS. 8–10. Schematic transects from the beach to the low tide line. FIG. 8: Eastern part characterized by an almost monospecific fauna and rocky substrate; FIG. 9: Central part characterized by sea grass and by an intensely bioturbated firm-ground zone; FIG. 10: Western part of the flat characterized by diverse fauna and islands with small coral reefs (Modified from Waite & Strasser, 2011, p. 227, fig. 2, © Springer-Verlag 2010; with kind permission from Springer Science & Business Media B. V.).



## RESULTS

## Environment

The sublittoral zone of the three small rocky islands offshore of the estuary are colonised by patchy fringing reefs of corals and sponges, which support a diverse nektonic and benthonic fauna. Macro-faunal diversity decreases towards the east, where just below the beachfront patches of rock and dead coral occur, which are, however, relatively barren and covered by algae. The sediment consists of fine sand to very fine sand, dominantly composed of quartz grains with a minor fraction of biogenic carbonate clasts. It is relatively well sorted with grain sizes varying between 0.05 and 0.35 mm. Skeletal carbonate grains are larger but are mainly found on the beach and are relatively rare on the flat. No clays are deposited in the intertidal regime. The sediment on the tidal flat is characterised by a 2–3 cm thick, superficial, oxidized layer of grey sand overlying an organic-rich, darker layer below.

The tidal flat shows a strong zonation (Fig. 1). In the near-shore zone innumerable ocy-pode crabs re-open and maintain their burrows during low tide. The near-shore zone is 30 m broad in the west. It gradually narrows to approximately 10–15 m in the central part and disappears altogether in the east (Figs. 8–10).

Small specimens (< 8 cm) of *T. duplicata* are common in the near-shore zone. Nassariid gastropods and hermit crabs, usually occupying the shells of cerithids, architectonicids, nassariids, as well as *T. terebra* and *T. duplicata*, are present along the expanse of the flat in the near shore and intermediate zones. In the intermediate and "turritelline" zones infaunal bivalves (Cardiidae and Veneridae), polychaetes, sea stars, crabs as well as strombid, muricid and naticid gastropods occur. In the west, astriclypeid (sand-dollar) echinoids are also common, however, they rapidly become less frequent towards the east and do not occur on the central and eastern parts of the flat. Archasterid sea stars are common on the central flat but disappear towards the east. Beyond the intermediate zone large turritellines are common down to the low tide line and into the marginally subtidal facies and these define the "turritelline zone". A strip along the low neap tide line, which comprises the marginal intertidal to marginal subtidal facies, is covered by wispy, thin sea grass. Approximately 15 m seawards of the low tide

line the sediment becomes stabilised by algal growth and immobile, forming a firmground that is intensely burrowed by crustaceans. No turritellines were encountered in this zone. During the study period, water temperature was generally around 28°C, visibility was between 30 cm and 4 m, and water chemistry showed normal marine conditions with a pH of 8.0 and salinity of 33‰.

## Turritellines

Shells of two different species of turritellines were found during this study. *Turritella duplicata* (Fig. 11) is common both as dead shells on



FIG. 11. *Turritella duplicata* (Linnaeus, 1758) ventral view. Scale bar = 2 cm.



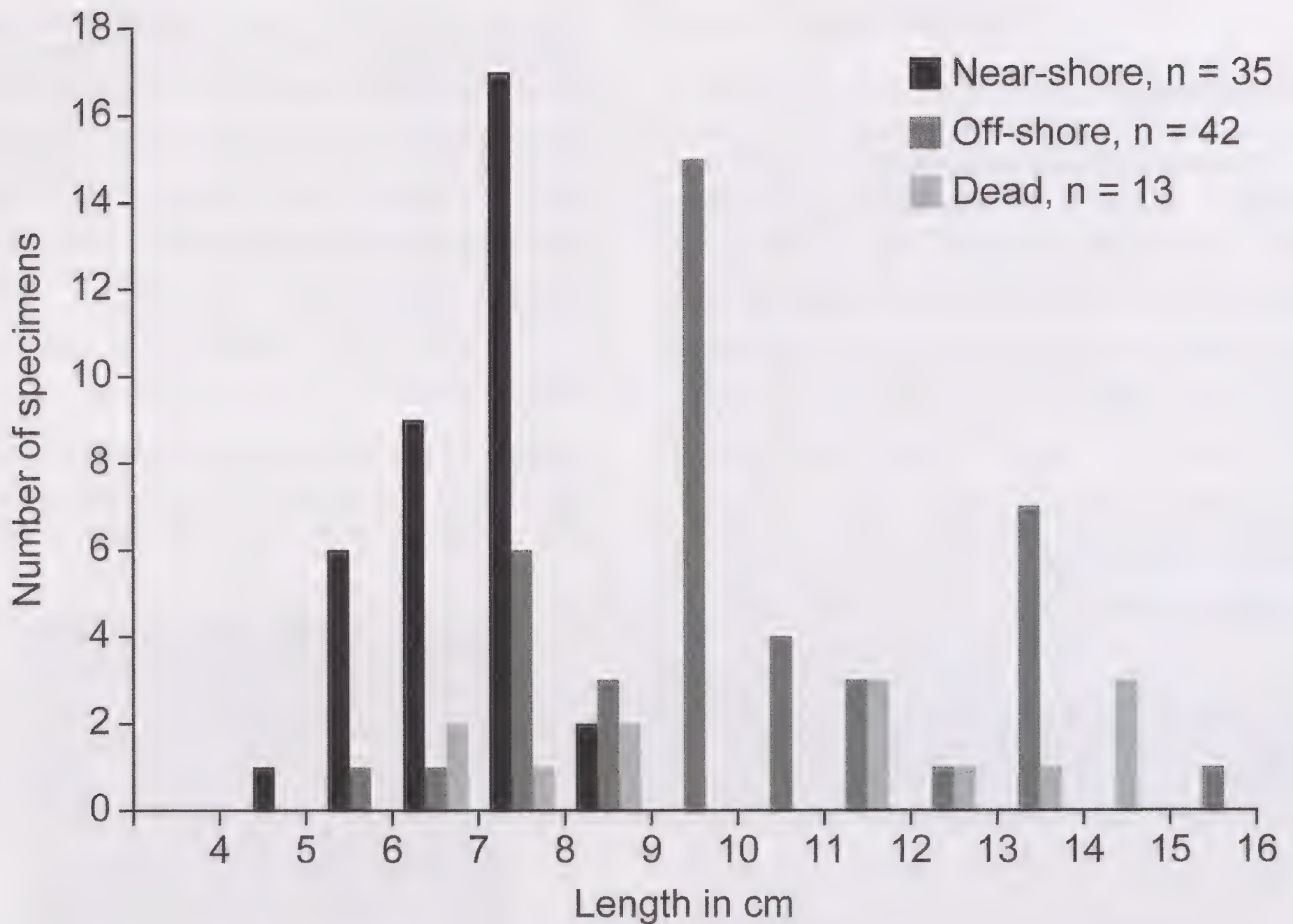


FIG. 12. Turritellid size distribution on the Nopparat Thara tidal flat ( $n = 90$ ). Smaller individuals generally inhabit a zone near to the shore whereas larger individuals prefer a habitat closer to the low tide line.

the beach and as living specimens on the tidal flat, whereas *Turritella terebra* (Linnaeus, 1758) was occasionally found dead on the beach. Unfortunately, due to heavy boat traffic along the coast, little information was obtained from the subtidal zone.

Live *Turritella duplicata* occur in two different zones on the flat. The near-shore zone is characterized by a population consisting of smaller specimens with shell-lengths between 5 and 9 cm (Fig. 12). Large specimens with shell-lengths between 9 and 16 cm (Fig. 12) are found further out on the flat, between 80 m from the beach and the sea grass in the west and 30 m from the beach up to the low-tide line in the east ("turritelline zone" in Fig. 1). The largest live specimens are found in the sea-grass meadows, at the low tide line beneath a constant cover of a few centimetres of water.

Four shallow excavations of the topmost 5 cm of sediment over an area of 9 m<sup>2</sup> were conducted at different points on the flat, to find live infauna and to support the zonation observed in the transects. Excavation (D1 in Fig. 1) in

the outer Turritelline zone revealed: eight sand-dollar echinoids (Astriclypeidae), four sea stars, one *T. duplicata* and one crab. Excavation (D2 in Fig. 1) also in the Turritelline zone yielded two *T. duplicata* and one crab. Excavation (D3 in Fig. 1) was in the intermediate zone and no macrofauna was found. In the east, no near-shore turritellines were observed and the tidal flat is narrower on account of its steeper inclination. Turritellines occur only in a narrow zone near the low tide line. Excavation (D4 in Fig. 1) revealed one single *T. duplicata*.

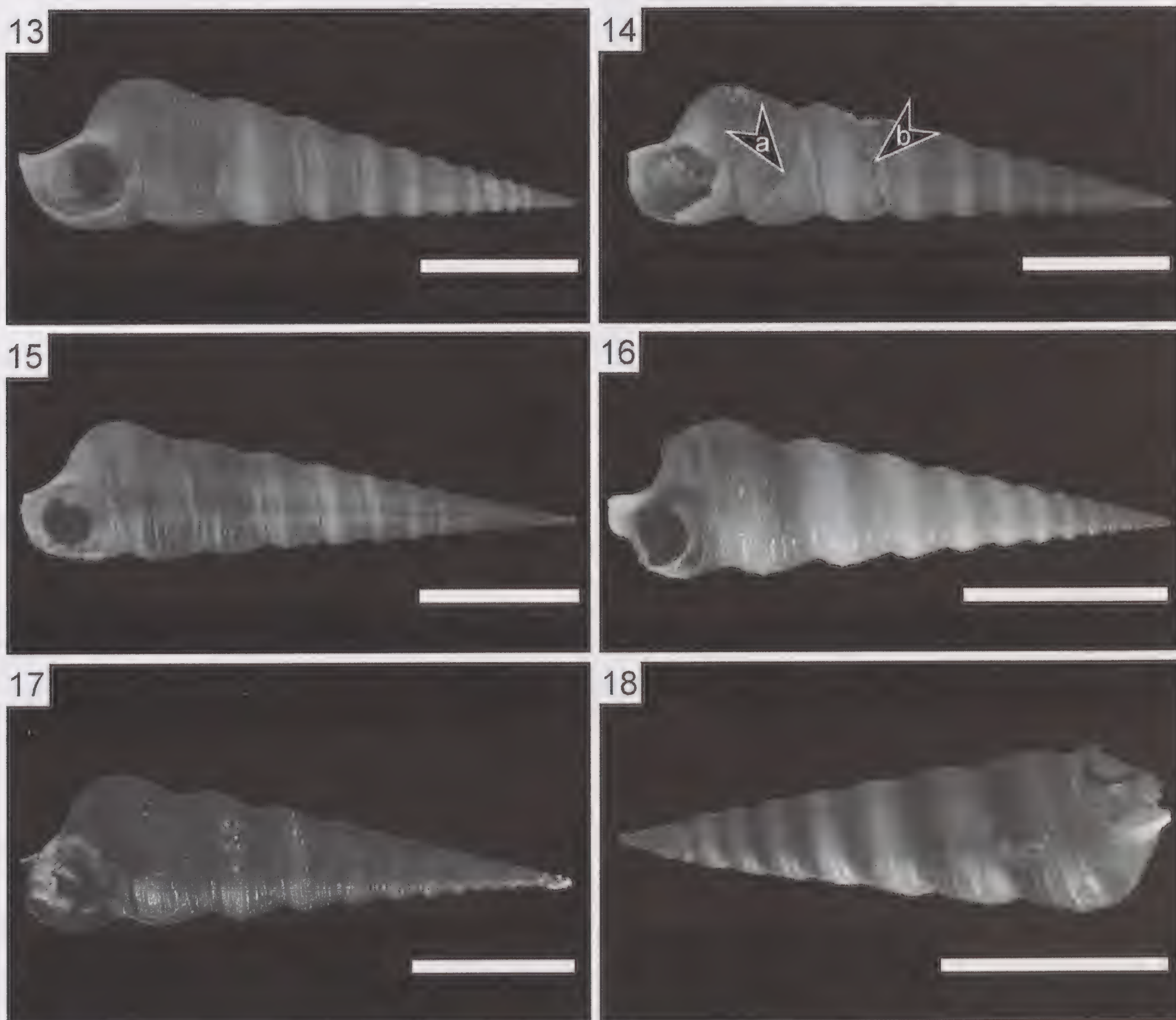
The near-shore population is exposed to currents and scouring during times of strong wave action. On one afternoon during particularly strong surf, over 30, rather small (6–7 cm long), live specimens of *T. duplicata* were thrown up onto the beach in the central part. This was the only time live specimens were encountered on the beach. Many of these remained immobile with the soft body retracted into the last whorl and the operculum loosely closed. A few, however, were highly active and were trying to make their way back into the water.



While almost all of these specimens showed slight damage to the aperture, only a few were significantly broken at apex or aperture or both (Figs. 13–18). During the following low tide a large number of specimens in the near-shore zone were encountered crawling along the surface. The animals moved across the sediment surface by extending the foot far out of the aperture and then dragging the shell behind, thereby achieving one “step” every 4–5 s and a speed of about 6 m/h. Direction seemed to be of minor importance, as specimens were frequently dislodged and rolled around by incoming waves, which caused involuntary direction changes. They kept moving with the same speed, seemingly unperturbed. As discussed by Allmon (1988) and contrary to the observa-

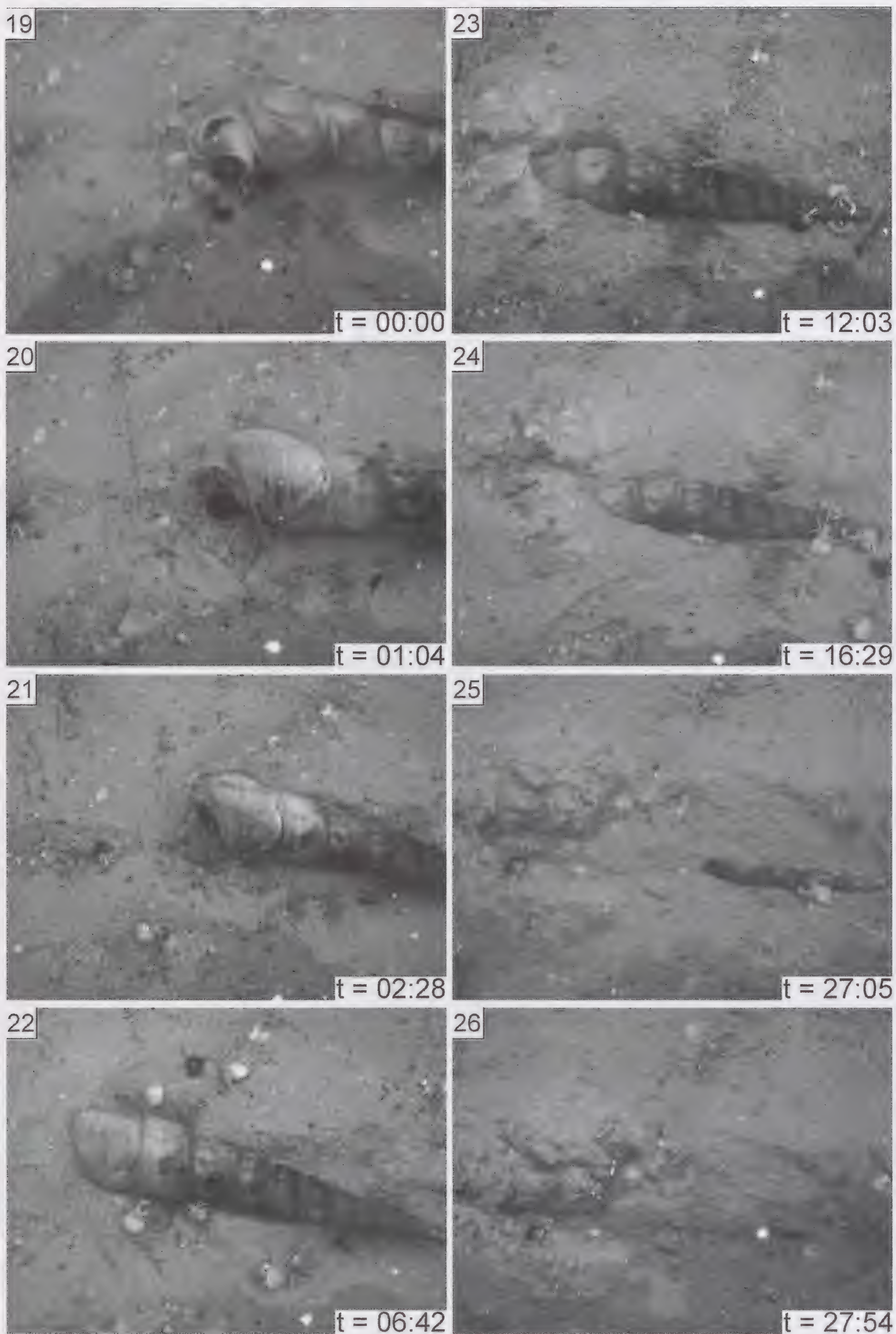
tions of many other authors (e.g., Young, 1946; Hickman, 1983; Kennedy, 1995), this indicates that turritellines can be very active.

Two specimens were observed burrowing. These were unearthed again, placed on the surface and then documented while reburying. The larger specimen (13.5 cm long, some apical whorls broken off; 3.5 cm basal diameter) took 32 min to become completely buried while partially covered by water (Figs. 19–26). The smaller specimen (5.3 cm long and 1.8 cm basal diameter) took 3 min and 50 s to bury itself and start feeding in 2 cm of water. Burrowing was achieved by extending the foot and pushing it into the sediment then pulling the shell in after it by rotating it about 30° to the right and then back again. The small specimen achieved



FIGS. 13–18. Six heavily damaged live specimens collected from the beach rubble in one afternoon during heavy surf. FIG. 14: Depicts a specimen that also shows two repaired scars: a = scar parallel to the apertural lip, b = jagged “can-opener” scar perpendicular to the growth lines.





FIGS. 19–26. Time laps image series of *T. duplicata* burying itself. T-values correspond to time elapsed after beginning of the burrowing. Specimen is 13.5 cm long and 3.5 cm in diameter at the aperture.



one cycle of pulling and twisting every 7–20 s. With the 12<sup>th</sup> cycle it rotated its shell 45° to the left and with the 13<sup>th</sup> cycle an additional 45° to the left positioning the aperture perpendicular to the sediment surface. Once in this position it began to circulate water through the mantle cavity almost immediately evidenced by two holes appearing at the surface and particles being sucked in.

The measured sample of snails plotted in Figure 11 likely represents but a fraction of the population on the flat. Close examination of the sediment surface revealed many buried individuals almost completely covered by sediment with just a small area of uncovered shell and two subcircular holes, corresponding to the excurrent and incurrent openings, visible at the surface (Fig. 27). Occasional individuals were also encountered in other orientations: lying completely exposed on the surface with the aperture facing down and the operculum loosely closing the aperture; moving across the sediment; or lodged apex-down in the sediment with the aperture raised 2–3 cm in the air above the sediment surface.

Dead shells on the flat were encountered in all states of preservation from practically pristine to severely fragmented or encrusted. Live specimens frequently showed repair scars along the whorls and up to three scars were recorded in a single specimen. Encrustation of live specimens was rarely observed and then mainly by algae. Dead specimens on the tidal flat were usually occupied by hermit crabs and heavily encrusted by barnacles, bryozoans, serpulids, bivalves and limpets. In the beach

TABLE 1. Isotope analysis, key values.

| Iso-<br>tope          | Speci-<br>men | Mini-<br>mum | Maxi-<br>mum | Range | Mean   |
|-----------------------|---------------|--------------|--------------|-------|--------|
| $\delta^{18}\text{O}$ | Td1           | -2.01‰       | -0.47‰       | 1.54‰ | -1.18‰ |
|                       | Td2           | -2.15‰       | -1.24‰       | 0.91‰ | -1.76‰ |
|                       | Td3           | -2.47‰       | -1.66‰       | 0.81‰ | -2.02‰ |
| $\delta^{13}\text{C}$ | Td1           | -0.70‰       | 0.66‰        | 1.36‰ | 0.26‰  |
|                       | Td2           | -0.90‰       | 0.56‰        | 1.46‰ | 0.11‰  |
|                       | Td3           | -0.19‰       | 0.75‰        | 0.94‰ | 0.25‰  |

rubble, complete shells were rare and small shells in the range of 1–4 cm were absent. Occasional small (< 1 cm) *T. duplicata* shells with damaged apertures were found on the proximal flat, all inhabited by hermit crabs. Empty shells in good condition on the flat were rare.

Oxygen and Carbon Stable Isotopes

The stable oxygen and carbon isotope profiles for each specimen are plotted in Figures 28–30 in standard fashion, with lighter (depleted) values toward the top.  $\delta^{18}\text{O}$  minimum values reach around -2.74‰ and maximum values extend to around -0.47‰, with significant differences in the mean values occurring between the three measured specimens. The  $\delta^{13}\text{C}$  values show similar ranges and significantly less variability between specimens than the oxygen values (Table 1).



FIG. 27. *Turritella duplicata* in feeding position. Picture was taken in about two metres water depth. Note the small section of exposed shell at the apical end (arrow on the left) and the two sub-circular holes for the inhalant and exhalent currents (arrows on the right).

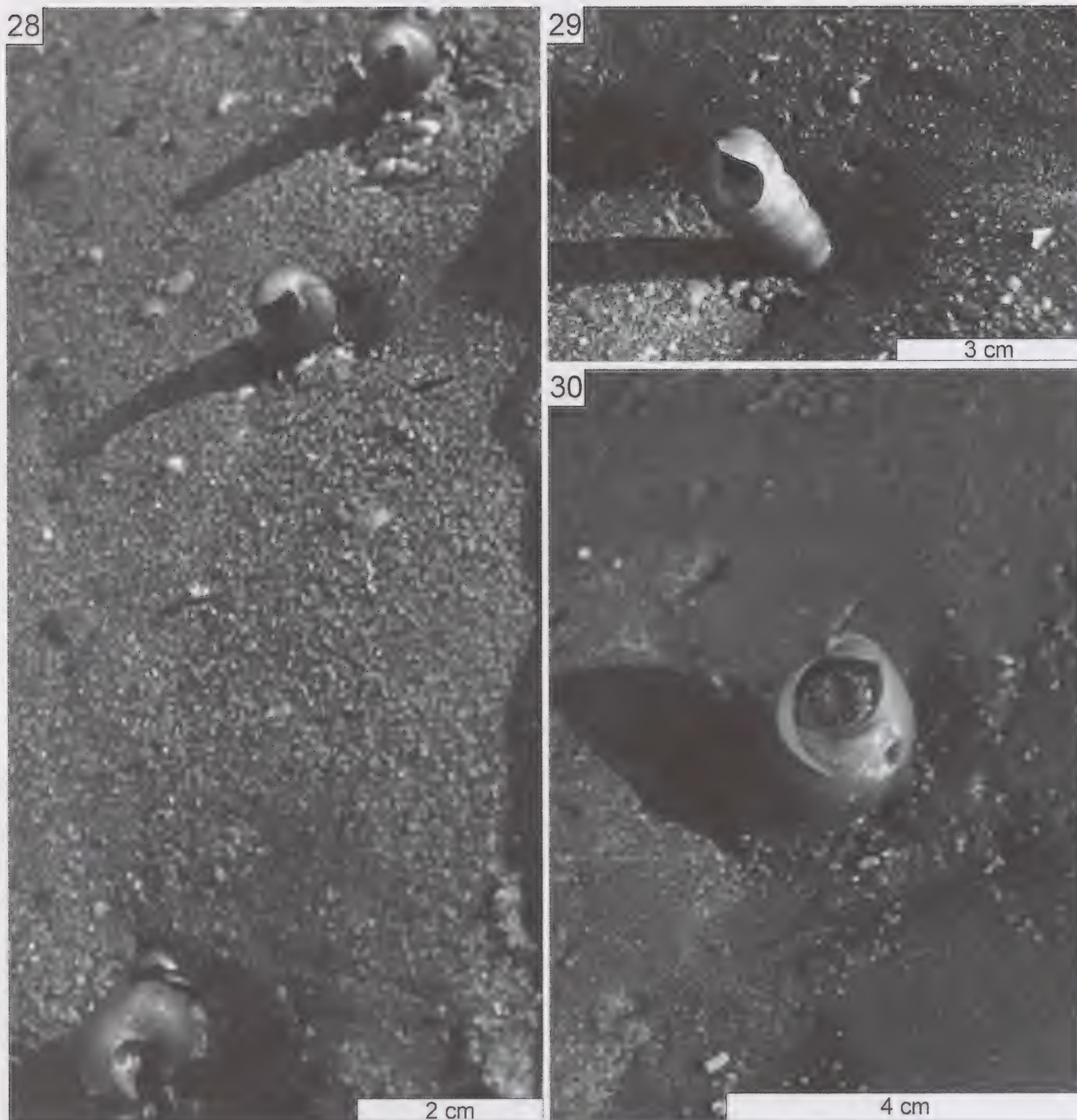


## DISCUSSION

## Position

Most live specimens of *Turritella duplicata* on the tidal flat adopt an infaunal position just beneath – with aperture oriented subvertical and long axis of the shell subparallel to – the sediment surface. A number of specimens were

observed oriented with the apex pointing down vertically or subvertically into the sediment (Figs. 28–30), an orientation that has also been noted previously by several authors (Allmon, 1988, 2011; Pinn, 1990; Waite & Strasser, 2011; Waite & Allmon, 2013; John Taylor, pers. comm., 2010). It is unlikely that this is an orientation the animals actively achieve, as the aperture often ends up well above the



FIGS. 28–30. Photographs of *T. duplicata* on the tidal flat at low tide with apices oriented down sub-vertically. FIG. 28: Three specimens lined up with equivalent orientations; FIGS. 29, 30: Close-ups of specimens with apertures sticking up to 3 cm out of the sediment. Pictures taken on Praphat tidal flat 70 km S of Ranong, Thailand, courtesy of John Taylor.



sediment where the animal is left incapable of moving the shell. However, observations on the flat during outgoing tide suggest that this position results from strong tidal currents that excavate the shell. When the apex is pointed in the direction of the sea the shell is progressively undercut and the spire is tilted into the sediment leaving the aperture sticking up. The fact that this position was not encountered during snorkelling indicates that wave action during incoming tide either reorients or buries the shells again so the animals can move and right themselves.

### Damage and Scarring

Of the 90 specimens documented during the study, 57 were in pristine condition and another 12 were categorized as only slightly damaged, and included specimens with a chipped aperture and/or minor damage to the apex. All but one of the live specimens ( $n = 8$ ) showing serious damage were collected from the beach rubble during one afternoon of strong surf. Six of the specimens showing the heaviest damage are depicted in Figures 13–18; all of these were found in the beach rubble. This suggests that battering in the high-water-energy surf zone is the primary agent responsible for inflicting the encountered damage. Conversely, Vermeij (1979), based on his own observations and those of other authors, suggested that most shell breakage in the tropics results from predation and not from abiotic causes. Vermeij (1978) noted that crustaceans frequently leave a characteristic spiral cut in snail shells when they attack (see also Shoup, 1968). Vermeij & Dudley (1982) counted repair scars in turritellines, describing them as “a wavy or angular discontinuity that cuts across the growth lines or axial sculpture of the gastropod shell”. They considered all such scars to be related to non-lethal attacks by durophagous predators. Later authors considered major breaks to correspond to substantial predator-induced injury in shallow-water species and that scars resulting from predation attempts by crabs are easily identified as jagged, “can-opener” breaks, which cross growth lines (Vale & Rex, 1988; Schmidt, 1989). This led Allmon et al. (1990), Cadée et al. (1997) and later Paul et al. (2013) to assume that the scars they were counting on turritellines exclusively resulted from lip-breakage or peeling by durophagous predators and were not related to abiotic agents.

The observations from this study, suggest that the physical energy of the environment is primarily responsible for the encountered damage and fracturing of the aperture. Many specimens in this study showed one or several scars or sites where shell growth had restarted after damage to the aperture had occurred (Fig. 14). When comparing the two scars in Figure 14 to the different forms of apertural damage documented in the beach specimens, it seems prudent to anticipate that apertural shell damage in tidal flat dwelling turritellines may easily result from abiotic factors and cannot convincingly be related exclusively to predation.

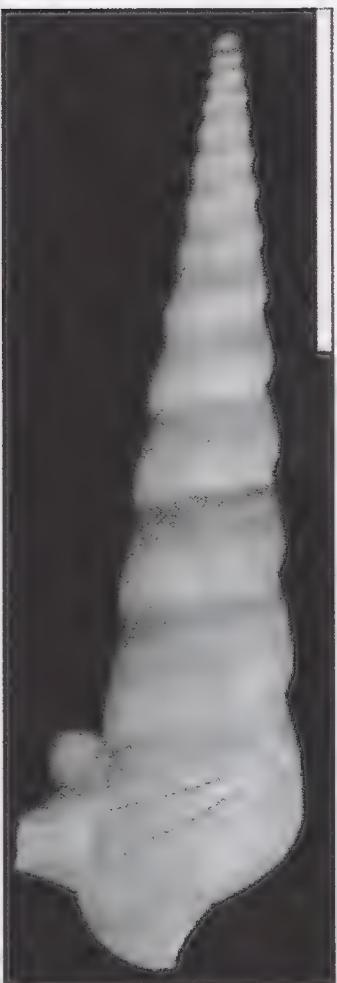
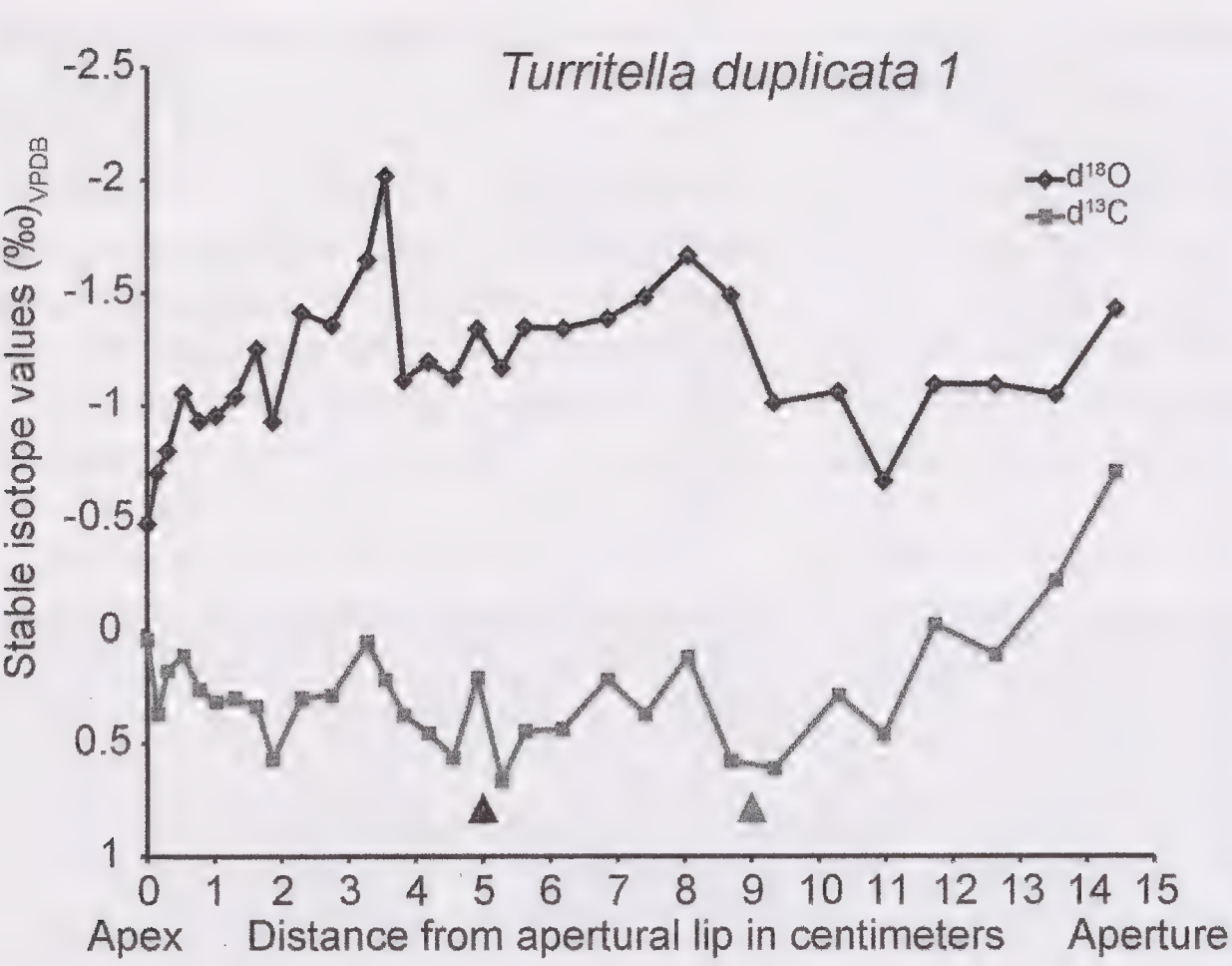
### Oxygen Isotopes and Age

Oxygen isotope sclerochronology has proven a successful tool in estimating age and growth rates for different fossil and living turritelline species (Allmon et al., 1992, 1994; Jones & Allmon, 1995). Recent estimates based on sclerochronological results suggest that individuals live to be between 1.5–3.0 years old and that growth is more rapid in juvenile stages (Allmon, 2011).

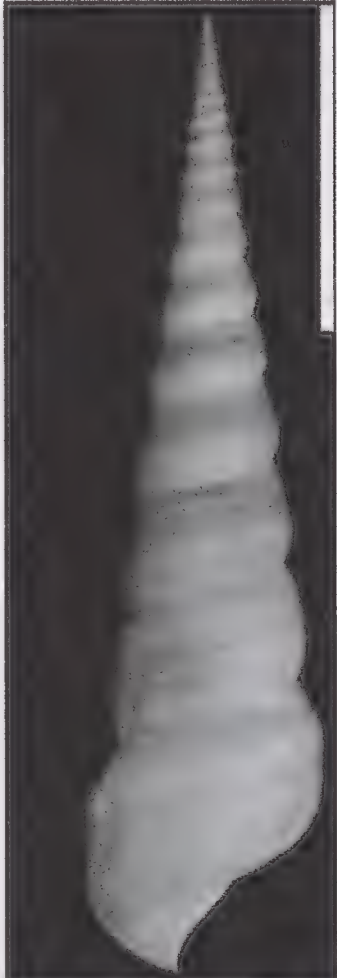
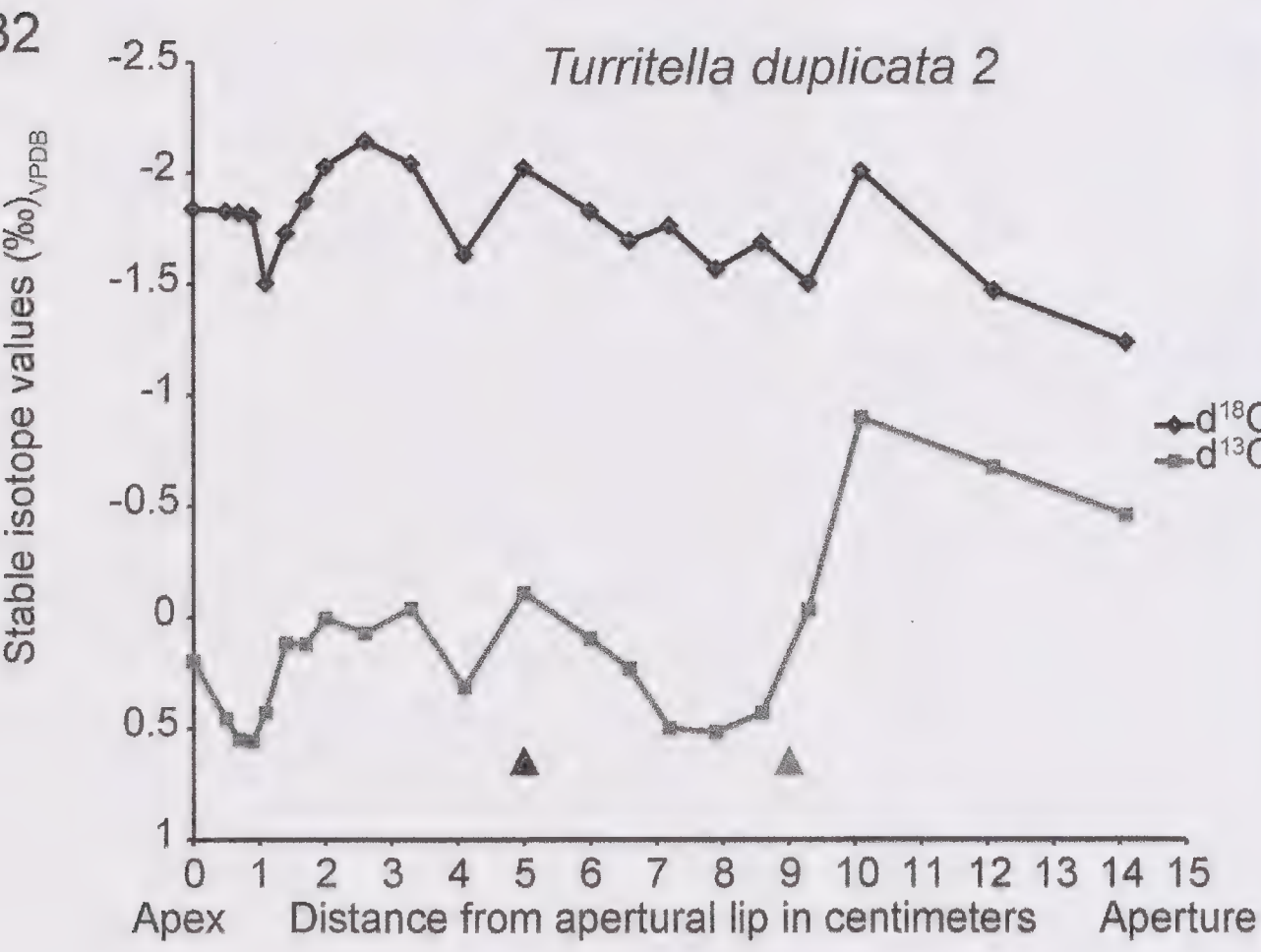
The  $\delta^{18}\text{O}$  value of mollusc shell carbonate is a function of the oxygen isotopic composition of the ambient seawater and the temperature at which precipitation occurs, with isotopically lighter shell carbonate being precipitated in warmer water (Grossman & Ku, 1986). In tropical areas seasonal temperature changes are minimal but heavy rainfalls associated with monsoonal wind patterns can strongly influence the isotopic composition of ocean water (e.g., Stephens et al., 2008). Changes in SST of maximally 4°C occur over the year in the Phang Nga Bay, but salinity along the east coast may vary by as much as 3.5‰ although for the southern part of the bay the variation is around 3‰ (Limpsaichol & Bussarawit, 1991). Therefore, the warm season when the isotopically lightest shell carbonate is formed coincides with the summer monsoon when precipitation and runoff of isotopically light meteoric water is at its highest. In the tropics the  $\delta^{18}\text{O}$  composition of rainwater is negatively correlated with the amount of rainfall (e.g., “amount effect”; Dansgaard, 1964; Fricke & O’Neil, 1999; Stephens & Rose, 2005). Therefore, the predominant driving forces for cyclical variations in the  $\delta^{18}\text{O}$  composition of shell carbonate in tropical waters are co-varying seasonal fluctuations in both temperature and degree of fresh water input into the ambient seawater (Figs. 31–33).



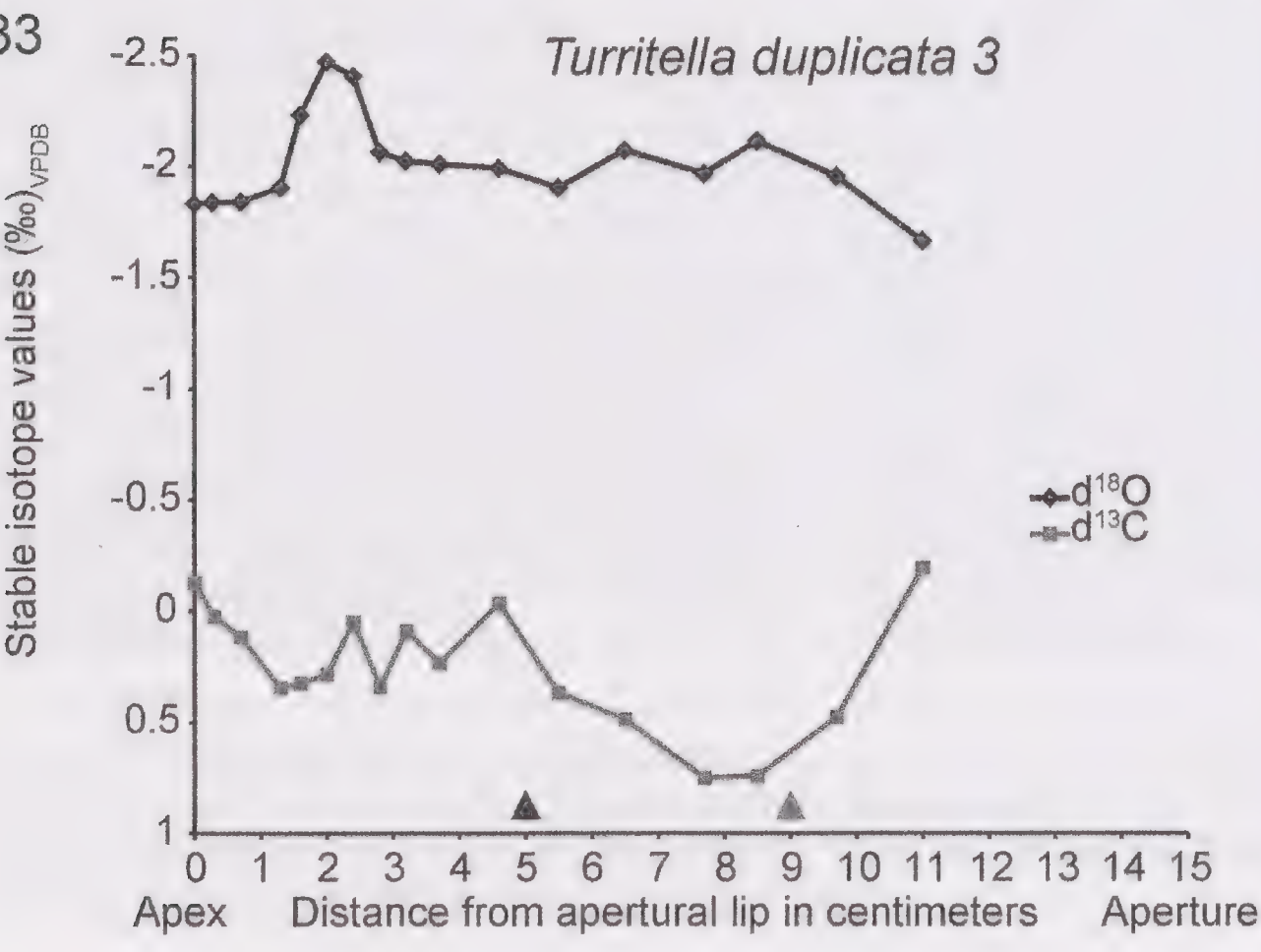
31



32



33





The  $\delta^{18}\text{O}$  composition at any given point of the shell reflects these water parameters at the time of secretion; hence it is possible to estimate the number of seasons a specimen has lived based on the number of annual cycles recorded in its shell. In the measured specimens, summer  $\delta^{18}\text{O}$  values reach around  $-2.24 \pm 0.23\text{‰}$  and winter values extend to around  $-1.06 \pm 0.59\text{‰}$ , with a total range of  $2.0\text{‰}$ . Molluscs that form their shells at near oxygen isotopic equilibrium with the composition of the ambient seawater (i.e., not showing significant fractionation due to vital effects) can be used as a proxy for estimating the temperature of the water during growth (Grossman & Ku, 1986).

A change of  $1\text{‰}$  in carbonate  $\delta^{18}\text{O}$  corresponds to a change of about  $4^\circ\text{C}$  in temperature (Anderson & Arthur, 1983). The two specimens recovered from the inner tidal flat show  $\delta^{18}\text{O}$  variations of  $0.91\text{‰}$  (*Td2*) and  $0.81\text{‰}$  (*Td3*). However, the third specimen, *Td1*, recovered from a more open-marine substrate offshore of the islands, shows a  $\delta^{18}\text{O}$  variation of  $1.54\text{‰}$ , which would indicate temperature variations of almost  $7^\circ\text{C}$ . Furthermore, the measured total range in  $\delta^{18}\text{O}$  of  $2\text{‰}$  is too large to be attributed to temperature fluctuations alone because it would suggest an annual range in ambient seawater temperature of approximately  $8^\circ\text{C}$ . This is four degrees more than the SST records can account for.

However, assuming equilibrium precipitation (Mook & Vogel, 1968) and a water composition of  $0\text{‰}$  for surface seawater in the Andaman Sea (Ravelo & Hillaire-Marcel, 2007), the aragonite paleotemperature equation for molluscs, established by Grossman & Ku (1986) provided a way to estimate the temperature regime under which calcification occurred:  $T^\circ\text{C} = 21.8 - 4.69 \times (\delta^{18}\text{O}_{\text{ar}} - \delta_w)$  with  $\delta^{18}\text{O}_{\text{ar}}$  = Oxygen isotopic composition of shell aragonite and  $\delta_w$  = Oxygen isotopic composition of sea water.

Substituting the average end-member  $\delta^{18}\text{O}$  values of  $-2.24$  and  $-1.06$  into this equation while assuming a composition of  $0\text{‰}$  for ocean water, yields a maximum (summer) temperature of  $32.3^\circ\text{C}$  and a minimum (winter) temperature

of about  $26.7^\circ\text{C}$ . These values overestimate the actual measured summer temperatures by about  $1^\circ\text{C}$ . However, the fresh water runoff responsible for the  $3\text{‰}$  salinity reduction during summer (Limpsaichol & Bussarawit, 1991) also changes the  $\delta_w$  composition. On the Andaman Islands, summer rainwater  $\delta^{18}\text{O}$  composition ranges from  $0.9$  to  $-5.4\text{‰}$  with a mean composition of  $-2.8$  (Laskar et al., 2011). A  $3\text{‰}$  reduction in salinity corresponds to  $\sim 8.6\%$  of fresh water being mixed into the ocean water. Assuming the summer ocean water and meteoric water  $\delta^{18}\text{O}$  compositions of  $0\text{‰}$  and  $-2.8\text{‰}$  respectively, the mixed water composition computes to  $-0.24\text{‰}$ . Introducing this value into the fractionation relationship (1) results in a summer SST of  $31.18^\circ\text{C}$ . This result well fits the recorded summer SST of  $31^\circ\text{C}$ .

The maximum recorded value of  $-0.47\text{‰}$  in specimen *Td1* would suggest temperatures as low as  $24^\circ\text{C}$ , a value well below any recorded temperature in the bay. Assuming equilibrium fractionation, the low winter values recorded in this specimen can only be explained by significantly positive  $\delta_w$  values. This suggests that the western end of the tidal flat – where specimen *Td1* was recovered – is influenced by more open marine waters with a positive isotopic composition during winter (e.g., Duplessy et al., 1981) than the rest of the tidal flat. An open-marine water influence is also supported by the observed differences in faunal composition at the west end of the tidal flat – where indicators of stenohaline conditions, such as echinoderms and corals, are abundant – compared to the progressively less diverse central and eastern parts of the tidal flat.

Based on the interpretation that the recorded cycles represent seasonal variations in the parameters of the ambient seawater, the measured specimens were between *Td3* = 2, *Td1* =  $2\frac{1}{2}$  and *Td2* = 3 years old, having hatched during the cool dry season.

For several turritelline species described in the literature, growth is seasonal, with the most rapid growth occurring during the warmest months, particularly in the first year of life (Bax et al., 2003). The reduction in shell growth may reflect an ontogenetic decline as more

←

FIGS. 31–33. Results of the stable isotope analysis. FIG. 31:  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  stable isotope profiles through specimen *Td1*; FIG. 32:  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  stable isotope profiles through specimen *Td2*; FIG. 33:  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  stable isotope profiles through specimen *Td3*. Black arrows mark the 50 mm growth stage. Grey arrows mark the 90 mm growth stage. Respective specimens are figured on the right, scale bars are 5 cm.



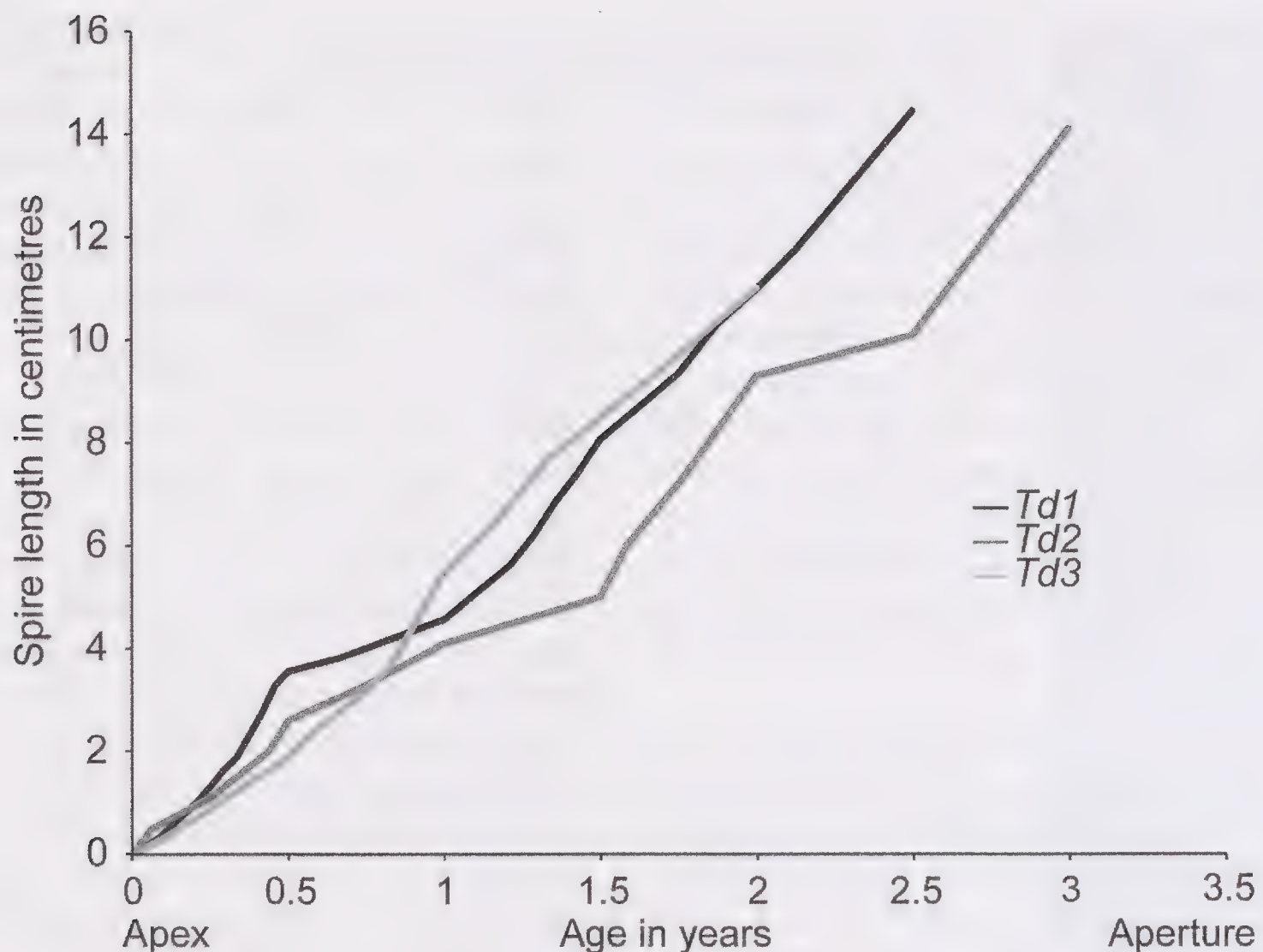


FIG. 34. Growth rate plot. Spire length in centimeters versus age as inferred from the seasonality in the oxygen isotope profile.

investment is put into reproduction (Allmon et al., 1992). Other authors suggest that a relatively fast growth rate in young specimens is advantageous to minimize lifetime spent in the size class most vulnerable to predation (Tull & Böhning-Gaese, 1993). The limited data available for growth rate and size-maturity relations suggest that caution should be used when drawing conclusions from one species to another.

The growth rate plots computed from the isotope data seem to confirm seasonal growth differences (Fig. 34). The two larger specimens show relatively clearly discernable differences in growth rate, while the smaller specimen shows relatively constant growth. Specimen *Td1* precipitated the initial 8 cm of the total spire length and, therefore, approximately 16 out of 19 preserved whorls in the first 1.5 years of life. This leaves the last three whorls or 6.4 cm respectively for the remaining year. However, within the first year 12 of the preserved whorls, or ~4 cm, were precipitated within the first half year of life. Similar observations can be made for the early growth stages in the other two specimens. This suggests a very high growth rate in very young individuals, especially when taking into account that the earliest whorls are missing in the larger specimens. The changes

in the slopes of the growth curves for specimen *Td2* suggest seasonal growth, with rapid growth occurring during the summer season (Fig. 34). This pattern is, however, less evident for the other specimens.

#### Size Distribution

The absence of specimens smaller than 5 cm during the observation period suggests that juveniles may not live on the flat at all. This is consistent with the idea that turritellines move over significant distances (hundreds to thousands of m) during their lifetime (Allmon, 1988). Therefore, either reproduction for this species is infrequent (once a year), and/or the juvenile specimens live in a different environment (e.g., deeper subtidal habitat, marsh/mangrove habitat). Reproduction is seasonal in all known turritelline species (Allmon, 2011). For example, *Turritella gonostoma* Valenciennes, 1832, in the Gulf of California is known to reproduce during early spring in shallow water (Allmon et al., 1992; Cadée et al., 1997) and only specimens larger than 4.2 cm occur in these tidal flat communities (Walker, 1998). Similarly, Waite & Allmon (2013) found shallow water populations of *Turritella leucostoma* Valenciennes, 1832, in the Gulf of California to



consist exclusively of specimens larger than 5 cm. It therefore seems likely that the population on the Nopparat Thara tidal flat represents a community of mature adults only. From the oxygen isotopic data it can be furthermore inferred that the three maxima in the live assemblage at 7, 10, and 13 cm in length correspond to three cohorts representing approximately 1, 2 and 3 years of age respectively.

On the flat two habitats can be distinguished, which are populated by individuals of different sizes. Smaller specimens, corresponding to ages younger than two years, preferentially inhabit a near-shore position on the tidal flat, whereas larger specimens, corresponding to approximately two years and older, preferentially inhabit the distal intertidal to marginal subtidal zones. No turritelline specimens were found in the proximal subtidal firmground zone. However, the presence of shells of *T. terebra*, which do not occur alive on the flat, points to the existence of a habitat in the distal subtidal zone. *Turritella terebra* is known to occur down to depths of about 30 m (Hickman, 1983; Poutiers, 1998).

#### Carbon Isotopes and Habitat

Carbon isotope data from shell precipitates of Recent molluscs are more complex to interpret than oxygen data because they are not only governed by physical parameters. Aquatic molluscs incorporate carbon from different sources into the shell. Additionally the so-called “vital effects”, related to changes in the biology of the animals, can change the proportion of the carbon derived from the various sources and play a significant role in the composition of the final precipitate (Grossman & Ku, 1986; Lorrain et al., 2004; Gillikin et al., 2007).

Isotopic changes through ontogeny, including trends to more negative values in shell  $\delta^{13}\text{C}$  with age, are common in both marine and freshwater molluscs (Lorrain et al., 2004; Gentry et al., 2008; McConnaughey & Gillikin, 2008). Many examples of  $^{13}\text{C}$ -depleted isotopic compositions have been attributed to vital effects (Grossman & Ku, 1986; Klein et al., 1996).

Vital effects can be distinguished into kinetic and metabolic vital effects. In aquatic molluscs  $^{13}\text{C}$ -depleted shell compositions attributed to kinetic vital effects, are caused by slower reaction kinetics for molecules containing the heavy isotopes. They involve simultaneous depletions in both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ , are favoured

by rapid skeletogenesis (McConnaughey, 1989a, 1989b), and are due to slower hydration and hydroxylation of  $\text{CO}_2$  molecules with heavy isotopes (McConnaughey et al., 1997). Although several studies of kinetic effects have shown no significant effect on aquatic mollusc shell composition (Klein et al., 1996; Lorrain et al., 2004), Butler et al. (2011) have recently argued that kinetic effects may be responsible for  $^{13}\text{C}$ -depleted values in juvenile bivalve shells with high growth rates. As molluscs generally precipitate at oxygen isotope equilibrium with their surroundings (Epstein et al., 1953; Chauvaud et al., 2005), kinetic effects should be minimal, and disequilibrium should be mainly due to metabolic effects.

Depletion of shell  $^{13}\text{C}$  composition attributed to metabolic vital effects are related to the activity of metabolism and caused by high rates of mantle metabolic pumping of respiratory  $\text{CO}_2$  to calcification sites (Klein et al., 1996). Metabolic effects have been suggested to be responsible for disequilibrium shell compositions, and especially depleted  $\delta^{13}\text{C}$  values in later ontogenetic stages, in different bivalves (Klein et al., 1996; Lorrain et al., 2004; Gillikin et al., 2007). This suggests that low metabolic activity forces the incorporation of carbon from seawater with an ambient DIC signal whereas when metabolic activity is high, more respiratory ( $^{13}\text{C}$ -depleted) carbon is supplied to the calcification sites and preferentially incorporated into the shell (Chauvaud et al., 2011). However, it should be noted that for some bivalves the metabolic contribution to the shell – at least for adult specimens – has been demonstrated to not vary significantly (Keller et al., 2002; Butler et al., 2011; Schöne et al., 2011; Beirne et al., 2012).

Aquatic molluscs incorporate carbon from both respired  $\text{CO}_2$  and ambient dissolved inorganic carbon (DIC) into their shells; the isotopic composition of the shells will depend on the composition – and the relative contribution – of the individual sources (Klein et al., 1996; Lécuyer et al., 2004; Lorrain et al., 2004; McConnaughey & Gillikin 2008; Chauvaud et al., 2011). Isotopically depleted carbon from respired  $\text{CO}_2$  is only believed to contribute approximately 10% to the shells of aquatic molluscs (McConnaughey et al., 1997), and their isotopic composition mainly reflects ambient DIC (Gentry et al., 2008; McConnaughey & Gillikin, 2008; Beirne et al., 2012). Depleted carbon isotope values in ambient DIC primarily result from the oxidation of organic matter



into bicarbonate ions in the ambient seawater (Lécuyer et al., 2004). Pore waters, in particular, are depleted in  $^{13}\text{C}$  due to the oxidation of organic matter, and this may influence the skeletal composition of infaunal molluscs (e.g., Lorrain et al., 2004; McConnaughey & Gillikin, 2008). Fresh water from runoff usually shows depleted DIC  $\delta^{13}\text{C}$  values on account of the decomposition of terrestrial organic matter with a light signature in the riverine water. The influence of fresh-water-derived, negative DIC on the composition of mollusc shells not living immediately in estuaries has been found to be of secondary importance for explaining variations in shell composition (Klein et al., 1996; Lécuyer et al., 2004; Chauvaud et al., 2011). However, Gentry et al. (2008) demonstrated a significant covariance of  $\delta^{13}\text{C}$  values and seasonal salinity in *Conus* shells, and Surge et al. (2001) found that for certain oysters,  $\delta^{13}\text{C}$  values can be used as a proxy for salinity. Populations of open ocean molluscs have in several instances been discerned from those of near-shore populations of the same species by their enriched  $\delta^{13}\text{C}$  composition (Lécuyer et al., 2004; Lorrain et al., 2004).

The  $\delta^{13}\text{C}$  data sets of the three specimens of *T. duplicata* studied here do not show clear cycles that could be related to seasonal changes in productivity and there is no apparent covariance between  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values, which might be attributed to changes in salinity related to fresh water runoff. However, all three specimens show a clear trend to lighter values in the later ontogenetic stages. A similar trend can be observed in the data of Allmon et al. (1992, 1994) and the data of Waite & Allmon (2013).

Only adult specimens of *T. duplicata* with shell lengths  $\geq 50$  mm were encountered alive in this study and nothing is known about the feeding habits, environment or biology of the juveniles. The black arrows in Figures 31–33 mark the 50 mm length on the measured shells and, therefore, the approximate age, for which it is inferred that the animals in question colonised the tidal flat. This point roughly corresponds to the end of the first cold season or about one year of age in the measured specimens. In specimens *Td2* and *Td3* it coincides with the beginning of a trend to heavier  $\delta^{13}\text{C}$  values. The grey arrows in Figures 31–33 mark the 90 mm length, which seems to roughly correspond to the second cold season or about two years of age. In all three specimens it marks the beginning of a strong decreasing trend in the  $\delta^{13}\text{C}$

values. This size also roughly corresponds to the size at which the majority of the individuals migrate to the outer tidal flat.

The measured specimens, therefore, show a change in the  $\delta^{13}\text{C}$  composition of the shells from high or even highest values at the end of their second year of life to lowest values in their third year of life with a range of up to 1.65‰. Describing a similar trend in the  $\delta^{13}\text{C}$  record of turritellines from the Gulf of California, Waite & Allmon (2013) suggested three possible causes for the observed systematic depletion. (1) The depletion occurs on account of the lighter composition of near shore versus offshore DIC. (2) The depletion is caused by a preferential ingestion of POC with a lighter composition. (3) The depletion is related to higher metabolic rates supplying more respiratory carbon to calcification sites.

The first explanation can probably be ruled out in the Nopparat Thara population as the animals are already living in a near shore setting at the beginning of their second year of life but the depletion does not occur until the end of the second year.

The second explanation cannot be ruled out. It can be noted, however, in comparison to the specimens in the Gulf of California, the Nopparat Thara specimens are significantly depleted in  $\delta^{13}\text{C}$ , indicating that they are feeding on light POC throughout their lives. Waite & Allmon (2013) argued that the trend was unlikely attributable to a change in food preference, as it would call for adult turritellines in the Gulf of California to feed exclusively on  $\text{C}_3$  plant debris. The  $\delta^{13}\text{C}$  composition of particulate organic matter on the Nopparat Thara tidal flat – although potentially variable throughout a single year depending on freshwater input – is expected to be relatively constant in the longer-term trend. Measured values for particulate organic carbon (POC) on the shelves of west Thailand are around -22 to -24‰ (Miyajima et al., 2009) consisting primarily of contributions by sea grass, mangroves and  $\text{C}_3$  land plants (Kuramoto et al., 2001). As habitat and biology are equivalent for adult specimens on the flat, and no systematic depletion is seen between juveniles and adults, selective feeding is unlikely to account for the systematic depletion in the  $\delta^{13}\text{C}$  values in the third year of life. Smaller variations in the shell record can easily be attributed to variations in the  $\delta^{13}\text{C}$  composition of food and ambient DIC related to freshwater input or seasonality and varying growth rates throughout the year.



The systematic trend, however, can only be satisfactorily explained by an enhanced contribution of metabolic carbon to shell secretion in the third year of life. Higher metabolic rates provide more light, respired CO<sub>2</sub> to the pool of carbon available for calcification, increasing the fraction of respired CO<sub>2</sub> relative to ambient CO<sub>2</sub> available for shell secretion. This might be related to maturity and reproduction (Allmon et al., 1992) or predation pressure (Tull & Böhning-Gaese, 1993). The effect might be especially important in the context of reduced growth rates in the later ontogenetic stages, as proposed by Allmon (2011).

The minimum increase in the proportion of metabolic carbon necessary to account for the observed change can be quantified by applying the simple model for derived shell  $\delta^{13}\text{C}$  fractions expressed in equation (1) of McConnaughey & Gillikin (2008):

$$R \times (\delta^{13}\text{C}_{\text{Org}}) + (1-R) \times (\delta^{13}\text{C}_{\text{Ambient}}) = (\delta^{13}\text{C}_{\text{Blood DIC}}) = (\delta^{13}\text{C}_{\text{Shell}}) - \Delta \text{ with}$$

$R$  = parts respired carbon;  $(\delta^{13}\text{C}_{\text{Org}})$  = carbon isotopic composition of respired carbon;  $(\delta^{13}\text{C}_{\text{Ambient}})$  = carbon isotope composition of ambient DIC.

When substituting the average values of +1‰ for ambient DIC (Mook & de Vries, 2001), and  $\Delta = +2.7\text{‰}$  (Romanek et al., 1992; McConnaughey & Gillikin, 2008) for aragonite fractionation from blood, and assuming a 22‰ isotopic composition for respired carbon (Kurahara et al., 2001; Miyajima et al., 2009), then the  $\sim 0.8\text{‰}$  rise from the minimum  $\delta^{13}\text{C}$  value of the first and second year to the minimum value in the third year corresponds to an increased incorporation of metabolic carbon of 3–4%.

Data on metabolic rates in turritellines are scarce. Fluorescein dye experiments performed on *Turritella gonostoma* have suggested relatively strong water pumping abilities, but measured rates of filtration in adult specimens of the same species from experiments in tanks suggested relatively low metabolic rates (Allmon et al., 1992). More data from tracer experiments are needed to estimate metabolic rates in turritellines and evaluate the potential of increased respiratory CO<sub>2</sub> being incorporated into the shell in adult specimens. Nevertheless, the gradual nature of the change to lighter  $\delta^{13}\text{C}$  values seems to coincide with the movement of the adults from the inner tidal flat to the outer tidal flat at the end of the second year of life and suggests a progressive modification of the fraction of light carbon incorporated into the shell.

## CONCLUSIONS

The studied tidal flat is inhabited by a population of semi-sessile, infaunal, adult *Turritella duplicata*. Subvertical positions of turritellids with apices pointed down into the sediment are thought to be related to tilting by tidal currents and not a result of active movement. The high proportion of damaged specimens collected on one day from the beach during high surf suggests that jagged can-opener scars can result from physical breakage by waves. Oxygen isotope sclerochronology and population size frequency distribution suggest that large individuals reach an age of three years and that the observed population consists of adults between approximately one and three years in age. Younger specimens preferentially colonise the inner tidal flat and move to the outer tidal flat towards the end of their second year of life. The carbon isotopic composition of the analysed shells shows a trend to lighter values at the end of the second year of life equivalent to a shell length of approximately 90 mm. Assuming that the water parameters and composition of POC cannot account for the variation in the long term trend, this can be explained by a 3–4% change in the proportion of respired metabolic carbon incorporated into the shell.

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## PREDATION ON RECENT TEREBRID GASTROPODS FROM THE INDIAN SUBCONTINENT AND A SPATIOTEMPORAL REAPPRAISAL BASED ON A REVISED GLOBAL DATABASE

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### ABSTRACT

Predator-prey interaction, especially drilling and shell-breaking predation pressure, caused significant evolutionary changes within these predator-prey communities. Although temporal trends are well understood in prey assemblages, studies to trace such changes within taxon-specific clades up to Recent times have been rare. Here, we studied both the drilling and shell-breaking predation on Recent terebrid gastropods from the Indian subcontinent and compared the results with a newly updated, global database. The major part of our data came from a large collection repositied in the archive of the Zoological Survey of India in Kolkata for more than 100 years.

Detailed analyses of this study based on a newly raised, global database revealed the following findings: (1) Drilling frequency (DF) of Indian terebrids was low, but consistent with the DF of only available but limited data provided by Vermeij et al. (1980). In comparison, peeling frequency (PF) in Indian terebrids appeared to be highest in the world; (2) DF showed latitudinal variation, that is, higher incidence of drilling occurred in higher latitudes; no such pattern emerged from the PF data; (3) drillholes were site-stereotyped, which suggested that Recent naticid drillers were escalated; (4) shell ornaments failed to protect against durophagy; (5) shell shape and thickness had different impact against different modes of predation. While slender and thicker shells were almost immune to drilling predation, no such relation existed for peeling predation; (6) on the other hand, body size appears to have evolved as anti-predatory traits in Recent terebrids. Larger species had low DF and high PF values; (7) temporally, DF showed fluctuating pattern, with modern values showing declining trend. This was perhaps due to increase in body size and behavioural change of the terebrid gastropods. Unfortunately, no peeling frequency data for this clade was available from the fossil record.

Key words: Recent terebrids, Gastropoda, predation, Indian subcontinent, spatiotemporal patterns.

### INTRODUCTION

Drilling and shell-breaking predation, which can be identified by characteristic traces made by the different groups of predators (Vermeij, 1987; Kowalewski, 2002; Harper & Kelly, 2012), has been extensively studied to test several aspects of predator-prey evolutionary dynamics in modern (Vermeij et al., 1980; Mondal et al., 2010a, 2014a; Paul et al., 2013; Das et al., 2014) as well as in the fossil record (Allmon et al., 1990; Kelley & Hansen, 1993, 2003; Mondal et al., 2014b; Mondal & Harries, 2015; Mallick et al., 2014, & references

therein). However, taxon-specific global studies on Recent molluscs are rare. Most of these published studies are from the western world (Vermeij et al., 1980; Tull & Bohning-Gease, 1993; Alexander & Dietl, 2001; Allmon et al., 1990), while works from the Indian subcontinent are few (Mondal et al., 2010a–b; Paul et al., 2013; Das et al., 2013; Chattopadhyay et al., 2014). Here, we attempted to make an updated dataset of predation (both drilling and peeling) on the gastropod family Terebridae to study many aspects of the predator-prey system at several taxonomic levels. Many recent workers (e.g., Allmon et al., 1990; Kelley &

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Hansen, 2006) also studied both lower (i.e., genus and species) and higher (i.e., family) taxon level predation on other groups.

The present specimens were obtained from the coastal regions of India and neighbouring countries (Myanmar, Sri Lanka, Mauritius, and Pakistan). Collections were made by many British workers before the independence of India in 1947 and were deposited in the archive of the Zoological Survey of India (ZSI), Kolkata, which we used to make our dataset (see also, Paul et al., 2013). The other part of our dataset came from literature sources (Vermeij et al., 1980; Signor, 1985; Funderburk, 2010), as well as from samples collected by us from eastern and western coasts of India. This compendium includes 100 species representing 15 genera within the family reported from all over the world (Appendix 1).

Terebrids are slender, turreted, sand- and mud- dwelling neogastropods, also known as auger shells. They may be smooth or axially and spirally ornamented and brightly coloured. They are mostly infaunal, their burrowing depth usually does not exceed the shell length (Venkitesan & Mukherjee, 2012). In the tropics, the majority of terebrids occur intertidally, while the shallow subtidal species can live up to about 350 metres of water depth (Venkitesan & Mukherjee, 2012). All terebrids are carnivorous, feeding on various worms (Miller, 1975).

Terebrid gastropods are important prey taxa for drilling and peeling predation in modern seas (Vermeij et al., 1980) and have a fossil record since the Cretaceous (Taylor et al., 1980). Vermeij et al. (1980) documented predation history on Recent terebrids and demonstrated latitudinal variation. They found that peeling predation is highest in the tropical Indo-West Pacific and lowest in warm temperate Atlantic areas. Vermeij et al. (1980) also found that peeling intensity was higher in slender shells than robust shells. They, however, recorded drilling frequency only in a few species from the Recent seas and found that modern level was achieved since the Eocene time; temporal data on peeling predation was not provided by them (Vermeij et al., 1980). They also concluded that increase of body size in Recent species took place as a response to resist naticid drilling predation. Signor (1985) also studied peeling predation on Recent terebrids and disputed the hypothesis of Vermeij et al. (1980), suggesting “that repair marks are not an adequate index of turritelliform shell’s vulnerability to durophagous predators” (for similar suggestion: Mondal

et al., 2014b; Mondal & Harries, 2015). Here, we estimated drilling and peeling predation intensities on Recent terebrid gastropods (n = 1,279) from the Indian subcontinent. We also updated the global data on terebrid predation and revisited the observations made by Vermeij et al. (1980).

MATERIALS AND METHODS

A global dataset of Recent predation on the family Terebridae was compiled mainly by assembling three major sources: (1) the Zoological Survey of India (ZSI) collection; (2) previously published literature data (Vermeij et al., 1980; Signor, 1985; Funderburk, 2010) and (3) new field collections from the eastern (Chandipur, Orissa) and western (Gulf of Kutch, Gujarat) coasts of India. We collected specimens during 2011–2012 (Fig. 1; Appendix 1). We analyzed a total of 1,279 specimens: 373 ZSI specimens, 706 specimens from our own collection, and 200 specimens from the published literature.

TABLE 1. Data of intensities of predation (drilling and peeling) on 15 most abundant Indian terebrid species (n = number of specimens; \*data not available; DF = Drilling Frequency; PF = Peeling Frequency).

| Species                        | Drilling predation |        | Peeling predation |     |
|--------------------------------|--------------------|--------|-------------------|-----|
|                                | n                  | DF (%) | n                 | PF  |
| <i>Diplomeriza spectabilis</i> | 637                | 47.4   | 637               | 0.8 |
| <i>Duplicaria duplicata</i>    | 69                 | 28.8   | 69                | 0.5 |
| <i>Granuliterebra persica</i>  | –*                 | –*     | 30                | 0.8 |
| <i>Hastula tenera</i>          | 16                 | 18.8   | 16                | 0.4 |
| <i>Hastula traillii</i>        | 156                | 0.3    | 255               | 1.0 |
| <i>Impages bacillus</i>        | 45                 | 12.5   | 45                | 1.4 |
| <i>Myurella affinis</i>        | 20                 | 26.3   | 39                | 0.9 |
| <i>Myurella nebulosa</i>       | 12                 | 0      | 25                | 1.1 |
| <i>Oxymeris crenulata</i>      | 21                 | 0      | 21                | 2.3 |
| <i>Oxymeris dimidiata</i>      | 13                 | 0      | 29                | 1.7 |
| <i>Oxymeris maculata</i>       | 13                 | 0      | 24                | 1.2 |
| <i>Terebra commaculata</i>     | 28                 | 0      | 40                | 1.0 |
| <i>Terebra</i> sp.             | 28                 | 14.6   | 28                | 1.1 |
| <i>Terebra subulata</i>        | 11                 | 0      | 11                | 1.8 |
| <i>Terebra tricolor</i>        | 10                 | 0      | 10                | 3.3 |
| Terebridae                     | 1,079              | 13.6   | 1,279             | 1.3 |



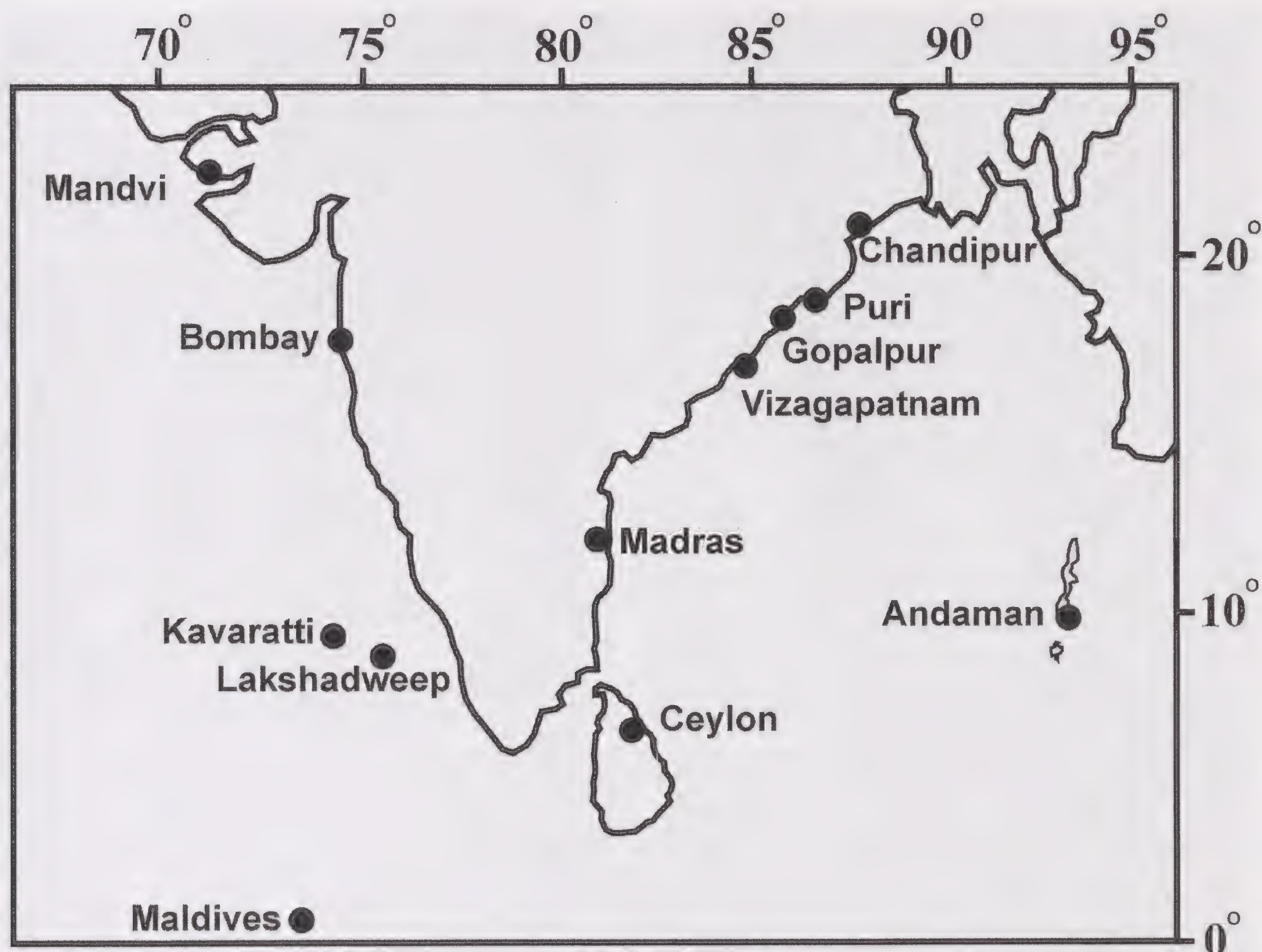


FIG. 1. Biogeographic distribution of abundant Recent terebrid species from Indian subcontinent.

Taxonomy of the family Terebridae was not stable until recently; Vermeij et al. (1980) followed a tentative classification. Subsequently, there appeared a thorough taxonomic revision of terebrids by Bratcher & Cernohorsky (1987). Recently, Venkitesan & Mukherjee (2012) revised taxonomy of the Indian terebrids, following Bratcher & Cernohorsky (1987). Here, we revised the ZSI and global data following Venkitesan & Mukherjee (2012), Castelin et al. (2012), Fedosov et al. (2014), Modica et al. (2014), and the World Register of Marine Species (WoRMS: <http://www.marinespecies.org/>) accordingly. The compendium included 32 Indian species in eight genera (*Diplomeriza*, *Duplicaria*, *Granuliterebra*, *Hastula*, *Impages*, *Myurella*, *Oxymeris*, and *Terebra*) (Appendix 1). Out of these 32 species, only 15 were abundant (i.e., represented by more than ten individuals; Vermeij et al., 1980) (Table 1). Our specimens were deposited in the Museum of the Department of Geological Sciences, Jadavpur University, Kolkata.

About 30% of the studied specimens came from the ZSI museum collection. Because old museum samples may be fraught with potential sampling bias (see also Allmon, 2005), it is likely that these samples, mainly collected for taxonomic studies by many famous British malacologists (e.g., Melvill & Sykes 1897; Smith, 1899; Preston, 1908, 1916), might have anthropocentric bias towards large and complete specimens (Roy et al., 2003; Hari et al., 2009). However, our previous (e.g., Paul et al., 2013) studies showed that ZSI collections are represented by both intact and broken specimens (apical or apertural parts missing; (Fig. 2) including corroded shells). Moreover, species are also characterized by specimens of varying ontogenetic stages. For these reasons, it is likely that the ZSI samples were relatively little affected by any kind of sampling bias (Paul et al., 2013; Das et al., 2013).

It has been argued that targeted sampling (i.e., collecting only the taxon of interest; for example, in many museum samples) may have



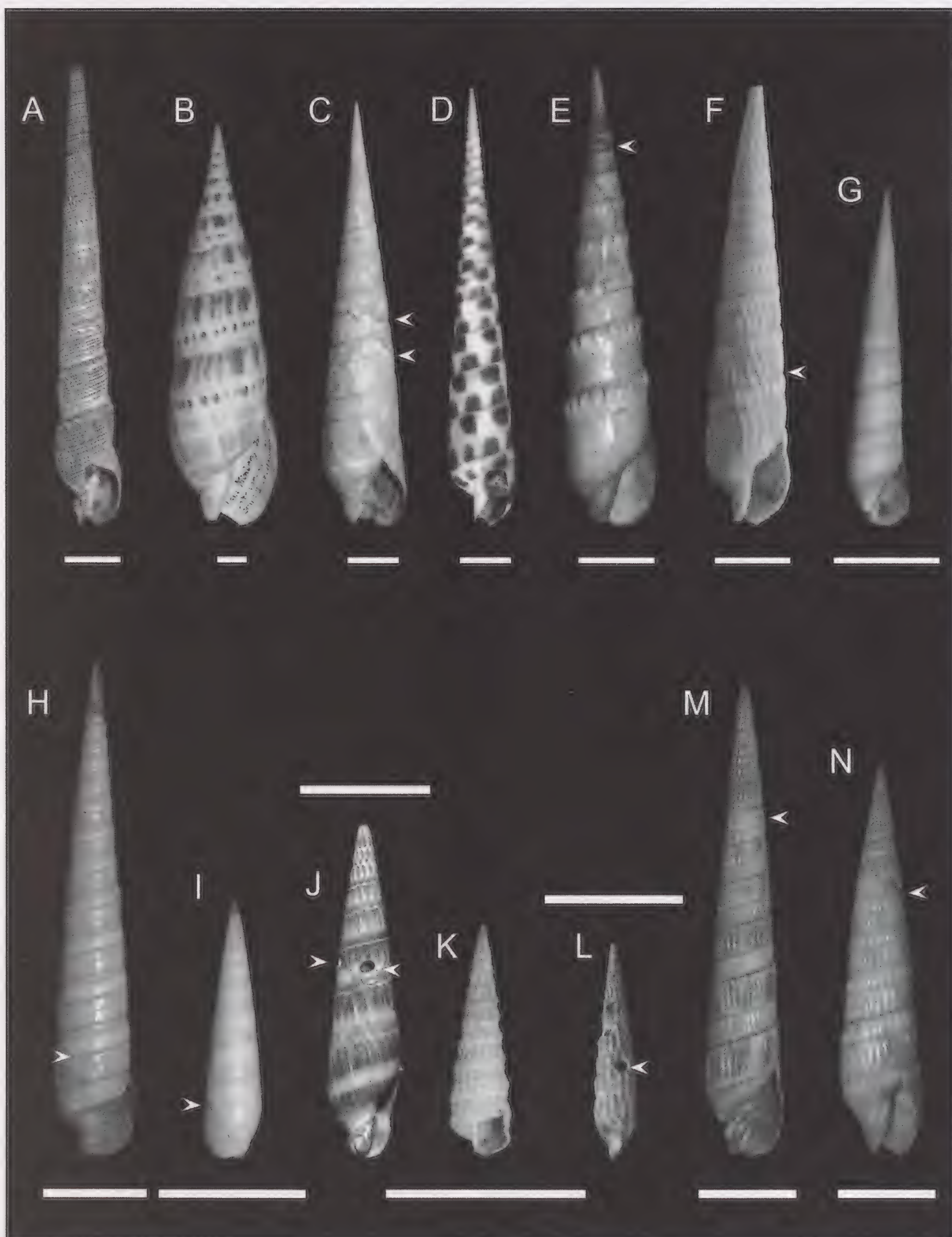


FIG. 2. 14 most abundant Indian species. A: *Terebra commaculata*; B: *Oxymeris maculata*; C: *O. dimidiata*; D: *T. subulata*; E: *O. crenulata*; F: *Myurella nebulosa*; G: *Hastula traillii*; H: *T. tricolor*; I: *Impages bacillus*; J: *Diplomeriza spectabilis*; K: *H. tenera*; L: *T. sp.*; M: *Duplicaria duplicata*; N: *M. affinis*. Data for *Granuliterebra persica* were obtained from Vermeij et al. (1980) and no specimen was available for photograph. A–D, fine and thick species; E–F, coarse and thick species; G–I, fine and thin species; J–N, coarse and thin species. Drillholes (J and L) and repair scars (C, E, F, H, I, M and N) were shown by arrows. All are apertural views except I. Scale bar = 1 cm.



significant difference in quantification of predation intensity in comparison with bulk sampling as the collectors could have discarded damaged shells including those with traces of predation. In contrary to this notion, many ZSI specimens show high frequencies of predatory marks like drillholes (Fig. 2J, L) or repair scars (Fig. 2C, E, F, H, I, M, N). Moreover, two recent studies (Ottens et al., 2012; Hattori et al., 2014) showed that collector's expertise has little impact on predation studies, further validating that the ZSI samples can be used in predation studies. Martinell et al. (2010) also demonstrated that museum material is useful even in quantitative study on predation.

The major portion of the specimens studied here (~ 55%) came from our own samples collected from the eastern and the western coasts of India (Fig. 1). For samples collected at Chandipur, on the east coast, we randomly collected all *Diplomeriza spectabilis* shells (following beach sampling protocol of Alexander & Dietl, 2001; Kelley & Hansen, 2007; Ottens et al., 2012) we encountered, along the five km long northeast-southwest directed siliciclastic beach (see Paul et al. 2013). Collection period included 3–4 hours each day, and we stayed for 5–7 days in two consecutive years (2011–2012). The field seasons were planned during full moon or new moon periods (during high tides), so that our beach collection would include adequate specimens. This collection of *Diplomeriza duplicata* ( $n = 637$ ) is the largest number for a single species of terebrid known from anywhere in the world (Appendix 1). For all these reasons, it can be argued that the present samples are equivalent to unbiased collections such as bulk samples (cf. Kowalewski, 2002). A similar approach was also undertaken for the collection of shells of *Duplicaria duplicata* from the Gulf of Kutch, western India.

Taphonomy might have significant effect on our predation study, mostly for museum and beach samples, because majority of the specimens considered here were likely collected dead. Drilled shells may behave differently during transportation and may be preferentially broken (Dudley & Vermeij, 1978; Roy et al., 1994; but see Hagstrom, 1996; Kaplan & Baumiller, 2000; Zuschin & Stanton, 2001). On the other hand, drilled shells may be better preserved, because a naticid takes its prey within the sediment before drilling (Edwards, 1974). Hermit crabs can also alter general trends of taphonomic preservation of shells, since they accept both infaunal and

epifaunal dead gastropod shells. Because of these complexities, it is difficult to separate out the selective effect of taphonomic overprinting between drilled and undrilled shells. Here, we assumed that the drilled and undrilled shells have equal preservation potential, following others (Dudley & Vermeij, 1978; Vermeij & Dudley, 1982; Allmon et al., 1990; Tull & Bohning-Gaese, 1993; Hagadorn & Boyajian, 1997; Paul et al., 2013).

In Chandipur, dead shells of *Diplomeriza spectabilis*, a subtidal species, were washed ashore during high tides along with many other gastropods and bivalves. In many bivalves, the ratio of right and left valve remained more or less equal, and it remained constant for decades (SB, personal observation). Even the naticid drilling frequency on various prey taxa (e.g., bivalve species, *Macra luzonica*) studied from 1990–2014 remained very conservative (DF about 20%) (see also Mondal et al., 2010a; Das et al., 2013). It further supported that our collected samples have minimum taphonomic overprinting.

The other source of our studied specimens for predation traces came from the sparse published literature on modern terebrid gastropods, almost all of which concentrated on shell-breaking predation, that is, on repair scars (e.g., Vermeij et al., 1980; Signor, 1985); while drilling predation data were rare (Appendix 1). Along with these modern data, we also collected temporal data on drilling predation so that we could compare our newly calculated global values of Recent predation with the intensities from the Eocene onwards (Vermeij et al., 1980; Fortunato, 2007; Appendix 1). Temporal data on peeling predation on terebrids are absent in the literature and could not be compiled here.

For the predation studies, two types of predation-induced scars were documented – drillholes and repair scars. Gastropod drillholes (both complete and incomplete), characterized by “truncated spherical paraboloids” (*Oichnus paraboloides*; Bromley, 1981), were generally attributed to naticid gastropod predation (Carriker & Yochelson, 1968; Bromley, 1981; but see Dietl et al., 2004). Drilling frequency (DF) was defined as percentage of shells with at least one complete drillhole divided by the total number of shells ( $n$ ) (Allmon et al., 1990). For this analysis, we used only complete or nearly complete (i.e., only apertural and or apical part partially broken) specimens ( $n = 1,279$ ). Incomplete drillholes speak to unsuccessful predation perhaps due to prey effectiveness (PE; see Vermeij, 1987; Kelly & Hansen, 2003;



TABLE 2. Size-specific predation intensity of 15 most abundant Indian terebrid gastropods (n = number of specimens; \*data not available).

| Species                        | Small specimens (< 4 cm) |        |     | Large specimens (> 4 cm) |        |     |
|--------------------------------|--------------------------|--------|-----|--------------------------|--------|-----|
|                                | n                        | DF (%) | PF  | n                        | DF (%) | PF  |
| <i>Diplomeriza</i>             | 637                      | 47.4   | 0.8 | 0                        | 0      | 0   |
| <i>Diplomeriza spectabilis</i> | 637                      | 47.4   | 0.8 | 0                        | 0      | 0   |
| <i>Duplicaria</i>              | 69                       | 28.8   | 0.5 | 0                        | 0      | 0   |
| <i>Duplicaria duplicata</i>    | 69                       | 28.8   | 0.5 | 0                        | 0      | 0   |
| <i>Granuliterebra</i>          | 30                       | –*     | 0.8 | 0                        | 0      | 0   |
| <i>Granuliterebra persica</i>  | 30                       | –*     | 0.8 | 0                        | 0      | 0   |
| <i>Hastula</i>                 | 172                      | 2.1    | 1.4 | 0                        | 0      | 0   |
| <i>Hastula tentera</i>         | 16                       | 18.8   | 0.4 | 0                        | 0      | 0   |
| <i>Hastula traillii</i>        | 156                      | 0.3    | 1.5 | 0                        | 0      | 0   |
| <i>Impages</i>                 | 45                       | 12.5   | 1.4 | 0                        | 0      | 0   |
| <i>Impages bacillus</i>        | 45                       | 12.5   | 1.4 | 0                        | 0      | 0   |
| <i>Myurella</i>                | 20                       | 26.3   | 1.2 | 12                       | 0      | 1.8 |
| <i>Myurella affinis</i>        | 20                       | 26.3   | 1.2 | 0                        | 0      | 0   |
| <i>Myurella nebulosa</i>       | 0                        | 0      | 0   | 12                       | 0      | 1.8 |
| <i>Oxymeris</i>                | 1                        | 0      | 1.0 | 46                       | 0      | 1.8 |
| <i>Oxymeris crenulata</i>      | 0                        | 0      | 0   | 21                       | 0      | 2.3 |
| <i>Oxymeris dimidiata</i>      | 0                        | 0      | 0   | 13                       | 0      | 1.7 |
| <i>Oxymeris maculata</i>       | 1                        | 0      | 1.0 | 12                       | 0      | 1.0 |
| <i>Terebra</i>                 | 33                       | 12.1   | 1.5 | 44                       | 0      | 1.6 |
| <i>Terebra commaculata</i>     | 0                        | 0      | 0   | 28                       | 0      | 1.1 |
| <i>Terebra</i> sp.             | 28                       | 14.6   | 1.1 | 0                        | 0      | 0   |
| <i>Terebra subulata</i>        | 0                        | 0      | 0   | 11                       | 0      | 1.8 |
| <i>Terebra tricolor</i>        | 5                        | 0      | 2.8 | 5                        | 0      | 3.8 |
| Terebridae                     | 1,007                    | 16.0   | 1.2 | 102                      | 0      | 2.3 |

but see Ansell & Morton, 1987; Hutchins & Herbert, 2013, for an alternative hypothesis where bivalve prey with incomplete borings were consumed by suffocation as well as through gapes). PE was calculated as the ratio between the number of incomplete drillholes and the number of total attempted holes (including both successful and unsuccessful drillholes; Vermeij, 1987). Presence of multiple drillholes could be a reflection of predator’s imperfection in prey handling, and was studied here (Kelley & Hansen, 2003). Multiple drilling frequency (MULT) was calculated as the proportion of drillholes that occurred in multiply bored specimens (Kitchell et al., 1986; Kelley & Hansen, 1993, 2006). For peeling predation, we studied the number of repaired scars (failed predation)

preserved on the dead shells. Aperture-parallel minor repairs were excluded, following Vermeij & Dudley (1982). In the similar way, for peeling frequency (PF), we calculated the ratio between the total numbers of repaired scars divided by the total numbers of specimens (Vermeij et al., 1980, 1982; Paul et al., 2013; Mondal et al., 2014b, c). The quantification of DF and PF was made only for abundant species (n ≥ 10) (Fig. 2; Table 1). Since predation frequency varies with prey size, we measured DF and PF for different size classes. For the global dataset, only two size categories were compared (“small” and “large”, i.e., < 4 cm and > 4 cm; Table 2). For the most abundant Indian species, *Diplomeriza spectabilis*, the same analyses were done by



TABLE 3. Size-specific predation intensity on *Diplomeriza spectabilis* from Chandipur (n = number of specimens).

| Size-class (mm) | n   | # of Scars | PF  | # of Successful Drillholes | DF (%) |
|-----------------|-----|------------|-----|----------------------------|--------|
| 10.10–20.00     | 131 | 61         | 0.5 | 89                         | 67.9   |
| 20.10–30.00     | 423 | 335        | 0.8 | 212                        | 50.1   |
| >30.00          | 83  | 138        | 1.7 | 20                         | 24.1   |
| Total           | 637 | 534        | 0.8 | 321                        | 47.4   |

classifying them into three subcategories (i.e., 10.1–20 mm, 20.1–30 mm, > 30 mm), because not only the species is abundant but all the complete specimens are of less than 4 cm size class and also to understand distribution of predation (Table 3).

To document spatial and latitudinal variability of predation, data were pooled for terebrid species from all over the world, all Indian subcontinental species, as well as only the abundant Indian species (n ≥ 10). Data on latitudes of the collected samples were gathered from Wikipedia (www.wikipedia.com) and were arranged into several latitudinal bins (10° interval) ranging from 0°–60° (Tables 4, 5). Although the entire Indian fauna belong to the tropical area, we wanted to understand any latitudinal variation of predation even in the Indian subcontinent. We therefore deliberately had chosen small latitudinal bin intervals. Data from the higher latitudes (> 60°) are not found in the published literature because temperate terebrids are only found in Australia and New Zealand (Vermeij pers. com., 2015). A few samples in Appendix 1 did not have specific information about localities (localities labeled broadly as India, Indian Ocean and Bay of Bengal in ZSI collections). They were excluded from the analysis.

TABLE 4. Latitudinal variation of predation intensity for terebrid species from all over the world (n = number of specimens).

| Latitudinal Bin | Species from all over the World |        |     |
|-----------------|---------------------------------|--------|-----|
|                 | n                               | DF (%) | PF  |
| 0°–10°          | 1916                            | 0      | 1.8 |
| 10°–20°         | 2103                            | 2.8    | 1.4 |
| 20°–30°         | 2164                            | 28.6   | 0.5 |
| 30°–40°         | 675                             | 0      | 0.9 |
| 40°–50°         | 223                             | -      | 0.5 |
| 50°–60°         | 4                               | 0      | 1.3 |

One of the measures of efficiency of drilling is the size selectivity and site stereotypy of drillholes (Kelly & Hansen, 1993). We selected three species (*Myurella affinis*, *Duplicaria duplicata* and *Diplomeriza spectabilis*) to determine the site and size stereotypy. The basis for selecting these three species was that they were most frequently drilled taxa (DF > 25%). We measured the position of drillholes in the vertical profile and radial quadrant systems to document whether the naticid predators were site-specific or not (Fig. 3; Allmon et al., 1990; Hagadorn & Boyajian, 1997; Paul et al., 2013; Mallick et al., 2014). To understand whether the recent predatory naticids were size selective, we plotted outer borehole diameter (OBD), which served as proxy for the predator size against prey shell height (Kitchell et al., 1981; Anderson et al., 1991).

For studies on prey defense against predation, prey shell ornamentation, apertural thickness and shell slenderness were calculated for the majority of the abundant prey species. To study the relationship between the prey shell ornamentation and predation intensity, a qualitative ornamentation scheme, based

TABLE 5. Latitudinal variation of predation intensity for all Indian and 15 abundant terebrid species (n = number of specimens).

| Latitudinal Bin | All Indian Species |        |     | 15 Abundant Species |        |     |
|-----------------|--------------------|--------|-----|---------------------|--------|-----|
|                 | n                  | DF (%) | PF  | n                   | DF (%) | PF  |
| 0°–10°          | 88                 | 14.1   | 1.4 | 44                  | 0      | 0.9 |
| 10°–20°         | 529                | 6.2    | 1.5 | 497                 | 5.6    | 1.3 |
| 20°–30°         | 708                | 47.5   | 0.5 | 715                 | 47.3   | 0.5 |



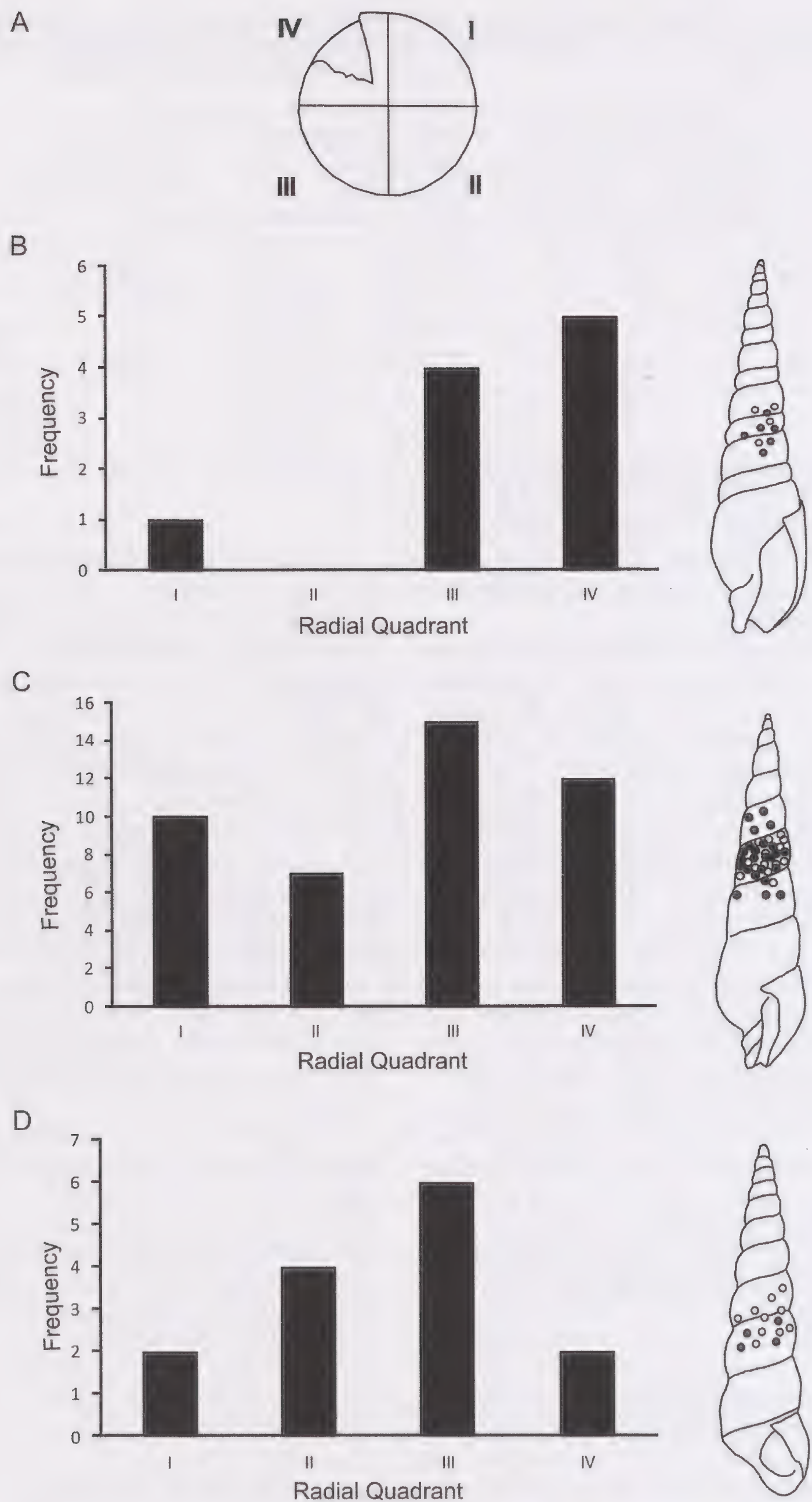


FIG. 3. Site stereotypy of three terebrid species. A: Showed the base of a terebrid shell indicating the distribution of different quadrants in radial system (cf. Allmon et al., 1990). B–D: Vertical and radial distributions of naticid drillholes. B: *Myurella affinis*; C: *Diplomeriza spectabilis*; D: *Duplicaria duplicata*. Solid circles represented drillholes on apertural side and open circles indicated drillholes on abapertural side. Note that the drillholes were highly stereotyped at the vertical profile, situated mostly in the middle part of the shell.



on strength of ornamentation of the shell, was adopted and compared with DF and PF (Table 6; cf., Paul et al., 2013). Species with smooth shell and fine thread-like ornamentation were grouped into Category 1 (i.e., finely ornamented), and species with prominent axial and/or spiral ornaments/subsutural nodes were pooled into Category 2 (i.e., coarsely ornamented) (Fig. 2). Apertural shell thicknesses were measured at the outer lip for 14 abundant species and were compared with the predation intensities. It may be argued that thickness at the outer lip may be an inappropriate measurement for evaluating antipredatory adaptation against drilling, because drillholes are highly site stereotyped at the middle of the shell, that is, second and third whorls from aperture. As mentioned above the study of ontogenetic change of shell thickness involves destruction of specimens and therefore we could not study thickness changes for the museum material.

For *Diplomeriza spectabilis*, we had sizable number of specimens and we did serial sectioning of several specimens to see ontogenetic thickness change. In all specimens, thickness is maximum in first and second whorls prior to the aperture where most of the drillholes were located and in all cases thickness is less at the apertural outer lip. Therefore, when we estimated thickness in the outer lip, it gives at least an idea about the minimum thickness in earlier growth stages. Average apertural thickness ranging from 0.1–0.5 mm was grouped into thin shell while shells with apertural thickness more than 0.5 mm were considered as thick shell (Table 7). Correlation between shell slenderness (i.e., maximum whorl diameter/shell height) and predation intensities was also studied (see Vermeij et al., 1980; Signor, 1985). Species with slenderness values greater than 0.16 were considered as “robust”, while species for which slenderness values were less than 0.16, were considered as “slender” (Fig. 2; Table 8). All these correlations were studied by using Spearman Rank correlation with  $\alpha = 0.05$ . Measurements were made with by digital callipers to the nearest 0.01 mm.

## RESULTS

For the present study, we listed predation frequencies of a total of 100 species under 15 genera within the family Terebridae from different biogeographic provinces of the world

(Appendix 1). Among them, only few were abundant in the Indian subcontinent, and were studied in detail. However, to document latitudinal variability of predation, we used both the global as well as Indian subcontinental data (see below).

### Drilling Predation

#### Drilling Frequency (DF)

In India, only 15 species were abundant. Out of them, four species belonged to the genus *Terebra*, three within the genus *Oxymeris*. *Hastula* and *Myurella* had two species each, while *Diplomeriza*, *Duplicaria*, *Granuliterebra* and *Impages* had one species each. The family level DF was 13.6% ( $n = 1,079$ ; Table 1). Within *Terebra*, *T. sp.* (DF = 14.6%,  $n = 28$ ) was most frequently drilled (Table 1), but the other species within this genus, that is, *T. subulata*, *T. commaculata* and *T. tricolor* were never drilled (Table 1). In *Hastula*, *H. tenera* had the highest drilling frequency of 18.8% ( $n = 16$ ), while *H. traillii* (DF = 0.3%,  $n = 156$ ) was less frequently drilled. Within the genus *Myurella*, *M. affinis* was most frequently drilled (26.3,  $n = 20$ ), but *M. nebulosa* showed no evidence of drilling ( $n = 12$ ). On the other hand, *Oxymeris* genus was never drilled (47). *Diplomeriza spectabilis*, *Duplicaria duplicata* and *Impages bacillus* showed DF of 47.4%, 28.8% and 12.5% respectively.

Incomplete (INC) and multiple drilling (MULT) were observed only on a few species (Table 9). Among them, the following species had more frequent incomplete holes: *Terebra commaculata* (INC = 4), *Hastula tenera* (INC = 5), *H. traillii* (INC = 4) and *Diplomeriza spectabilis* (INC = 13). However, when prey effectiveness (PE) was calculated, *T. commaculata*, *Oxymeris crenulata*, *O. dimidiata* and *T. tricolor* had high PE (PE = 1); the other four species had PE values ranging from 0.04–0.6 (Table 9). Interestingly, although the total number of INC in *D. spectabilis* was highest, PE value for this species was lowest (Table 9). Multiple drillholes were observed only on a single species, *Diplomeriza spectabilis* (MULT = 0.3; total number of specimen with multiple holes = 46).

The family-level DF showed considerable variation during ontogeny. When we divided family level data on the basis of two size classes (< 4 cm and > 4 cm) smaller specimens showed relatively higher frequency of drilling



TABLE 6. Relationship between shell ornamentation and predation intensity (n = number of specimens; \*data not available).

|        |  | Species                         | n   | DF (%) | n   | PF  |
|--------|--|---------------------------------|-----|--------|-----|-----|
| Fine   |  | <i>T. subulata</i>              | 11  | 0      | 11  | 1.8 |
|        |  | <i>O. dimidiata</i>             | 13  | 0      | 29  | 1.7 |
|        |  | <i>O. maculata</i>              | 13  | 0      | 24  | 1.2 |
|        |  | <i>T. tricolor</i>              | 10  | 0      | 10  | 3.3 |
|        |  | <i>T. commaculata</i>           | 28  | 0      | 40  | 1.0 |
|        |  | <i>H. traillii</i>              | 156 | 0.3    | 255 | 1.0 |
|        |  | <i>I. bacillus</i>              | 45  | 12.5   | 45  | 1.4 |
|        |  | All finely ornamented species   | 276 | 1.8    | 414 | 1.6 |
| Coarse |  | <i>M.affinis</i>                | 20  | 26.3   | 39  | 0.9 |
|        |  | <i>O. crenulata</i>             | 21  | 0      | 21  | 2.3 |
|        |  | <i>M. nebulosa</i>              | 12  | 0      | 25  | 1.1 |
|        |  | <i>G. persica</i>               | —*  | —*     | 30  | 0.8 |
|        |  | <i>H. tenera</i>                | 16  | 18.8   | 16  | 0.4 |
|        |  | <i>Duplicaria duplicata</i>     | 69  | 28.8   | 69  | 0.5 |
|        |  | <i>Diplomeriza spectabilis</i>  | 637 | 47.4   | 637 | 0.8 |
|        |  | <i>T. sp.</i>                   | 28  | 14.6   | 28  | 1.1 |
|        |  | All coarsely ornamented species | 803 | 19.1   | 865 | 0.9 |

TABLE 7. Relationship between apertural thickness and predation, shown only for Indian abundant species (n = number of specimens; \*data not available).

|       |  | Species                        | n   | DF (%) | n     | PF  | Average Apertural Thickness |
|-------|--|--------------------------------|-----|--------|-------|-----|-----------------------------|
| Thin  |  | <i>Duplicaria duplicata</i>    | 69  | 28.8   | 69    | 0.5 | 0.28                        |
|       |  | <i>T. tricolor</i>             | 10  | 0      | 10    | 3.3 | 0.31                        |
|       |  | <i>I. bacillus</i>             | 45  | 12.5   | 45    | 1.4 | 0.32                        |
|       |  | <i>H. traillii</i>             | 156 | 0.3    | 255   | 1.0 | 0.36                        |
|       |  | <i>H. tenera</i>               | 16  | 18.8   | 16    | 0.4 | 0.38                        |
|       |  | <i>Diplomeriza spectabilis</i> | 637 | 47.4   | 637   | 0.8 | 0.44                        |
|       |  | <i>M. affinis</i>              | 20  | 26.3   | 39    | 0.9 | 0.45                        |
|       |  | <i>T. sp.</i>                  | 28  | 14.6   | 28    | 1.1 | 0.45                        |
|       |  | All thin species               | 981 | 18.2   | 1,099 | 1.2 | —                           |
| Thick |  | <i>T. commaculata</i>          | 28  | 0      | 40    | 1.0 | 0.54                        |
|       |  | <i>T. subulata</i>             | 11  | 0      | 11    | 1.8 | 0.57                        |
|       |  | <i>M. nebulosa</i>             | 12  | 0      | 25    | 1.1 | 0.61                        |
|       |  | <i>O. dimidiata</i>            | 13  | 0      | 29    | 1.7 | 0.65                        |
|       |  | <i>O. crenulata</i>            | 21  | 0      | 21    | 2.3 | 0.88                        |
|       |  | <i>O. maculata</i>             | 13  | 0      | 24    | 1.1 | 1.03                        |
|       |  | All thick species              | 98  | 0      | 150   | 1.5 | —                           |
|       |  | <i>G. persica</i> *            | —*  | —*     | 30    | 0.8 | —*                          |



TABLE 8. Relationship between shell slenderness and predation intensity for 15 abundant Indian species (n = number of specimens; \*data not available).

|         | Species                        | n   | DF (%) | n   | PF  | Slender-<br>ness |
|---------|--------------------------------|-----|--------|-----|-----|------------------|
| Slender | <i>T. commaculata</i>          | 28  | 0      | 40  | 1.0 | 0.13             |
|         | <i>H. traillii</i>             | 156 | 0.3    | 255 | 1.0 | 0.15             |
|         | <i>T. tricolor</i>             | 10  | 0      | 10  | 3.3 | 0.16             |
|         | All slender species            | 194 | 0.1    | 305 | 1.8 | -                |
| Robust  | <i>O. dimidiata</i>            | 13  | 0      | 29  | 1.7 | 0.19             |
|         | <i>Duplicaria duplicata</i>    | 69  | 28.8   | 69  | 0.5 | 0.20             |
|         | <i>T. subulata</i>             | 11  | 0      | 11  | 1.8 | 0.20             |
|         | <i>M. nebulosa</i>             | 12  | 0      | 25  | 1.1 | 0.20             |
|         | <i>I. bacillus</i>             | 45  | 12.5   | 45  | 1.4 | 0.21             |
|         | <i>O. crenulata</i>            | 21  | 0      | 21  | 2.3 | 0.22             |
|         | <i>M. affinis</i>              | 20  | 26.3   | 39  | 0.9 | 0.26             |
|         | <i>T. sp.</i>                  | 28  | 14.6   | 28  | 1.1 | 0.23             |
|         | <i>H. tenera</i>               | 16  | 18.8   | 16  | 0.4 | 0.27             |
|         | <i>O. maculata</i>             | 13  | 0      | 24  | 1.2 | 0.28             |
|         | <i>Diplomeriza spectabilis</i> | 637 | 47.4   | 637 | 0.8 | 0.67             |
|         | All robust species             | 885 | 13.2   | 944 | 1.0 | -                |
|         | <i>G. persica</i> *            | -*  | -*     | 30  | 0.8 | -*               |

(DF = 16%; n = 1007), while larger shells (n = 102) were never drilled (Table 2). This general pattern is also true for individual genera: 14.6% versus 0% in *Terebra*, and 26.3% versus 0% in *Myurella* (Table 2). Even in *D. spectabilis*, for which all specimens were subdivided into three size classes (see Material and Methods), smaller specimens (10.10–20 mm, n = 89) had the highest value of DF (67.9%), as compared to the size class of greater than 30 mm (DF = 24.1%, n = 20), while the intermediate size class showed DF of 50.1% (n = 212). Rest of the genera however belonged to only one size class and therefore size-predation comparison could not be performed.

Latitudinal Variability of Drilling Predation

The global dataset on DF revealed fluctuating pattern with latitude; DF was highest within the 20°–30° latitudinal bin, decreased towards both higher and lower latitudes (Table 4). When DFs of all Indian species were pooled together, an exactly similar trend was observed (Table 5). We did not have sufficient number of specimens from higher latitudes (> 50°) to study that trend further (Table 4). Interestingly, there prevailed a distinct trend when DFs of

all Indian abundant species were considered, which showed an increasing trend of DF with increasing latitude (Table 5).

Behavioural Stereotypy of Drilling Predation

We studied the site and size stereotypy of predation on *Diplomeriza spectabilis*, *Dupli-*

TABLE 9. Record of incomplete (INC) and multiple (MULT) drillholes data for eight abundant Indian species.

| Species                        | INC (# of Attempts) | PE   | MULT(# of Individuals) |
|--------------------------------|---------------------|------|------------------------|
| <i>T. commaculata</i>          | 4 (4)               | 1    | 0                      |
| <i>O. crenulata</i>            | 2 (2)               | 1    | 0                      |
| <i>O. dimidiata</i>            | 1(1)                | 1    | 0                      |
| <i>T. sp.</i>                  | 1(2)                | 0.50 | 0                      |
| <i>H. tenera</i>               | 5 (8)               | 0.63 | 0                      |
| <i>H. traillii</i>             | 4 (52)              | 0.08 | 0                      |
| <i>Diplomeriza spectabilis</i> | 13 (325)            | 0.04 | 0.33 (46)              |
| <i>T. tricolor</i>             | 3 (3)               | 1    | 0                      |



*caria duplicata* and *Myurella affinis*. In vertical profile, drillholes were mostly located in the middle part, that is, second and third whorls from aperture for all three species (Fig. 3). In radial quadrant system (Fig. 3) drillholes were equally distributed in both apertural (I and IV) and abapertural (II and III) sides in case of *Diplomeriza spectabilis* (chi-square test,  $p = 0.47$ ). However, in *M. affinis*, the distribution of drillholes was selective mostly on the apertural side (chi-square test,  $p = 0.03$ ), but in *Duplicaria duplicata* majority of the drillholes were randomly distributed (chi-square test,  $p = 0.10$ ). When size selectivity of predation was studied by plotting outer drillhole diameter (OBD) against prey height, size selectivity showed poor correlation for all the above three species (Fig. 4).

#### Shell Ornamentation and Drilling Predation

Table 6 showed that drilling frequency increased with strength of ornamentation. The average DF of species with fine ornaments (Category 1) was 1.8%, whereas in coarsely ornamented species (Category 2), DF was significantly higher (19.1%; t-test,  $p = 0.02$ ). Within Category 1, two genera, *Terebra* ( $n = 49$ ) and *Oxymeris* ( $n = 26$ ) were never drilled, while *Impages* showed relatively higher DF (12.5%;  $n = 45$ ). In contrast, in Category 2, all of the five genera showed moderate to high values of DF (*Terebra*, DF = 14.6%,  $n = 28$ ; *Myurella*, DF = 16.6%,  $n = 32$ ; *Hastula*, DF = 18.8%,  $n = 16$ ; *Duplicaria*, DF = 28.8%,  $n = 69$ ; and, *Diplomeriza*, DF = 47.4%,  $n = 637$ ) except *Oxymeris* which was never drilled (DF = 0,  $n = 21$ ). Within *Myurella*, *M. affinis* was the most frequently drilled (DF = 26.3%,  $n = 20$ ), whereas *M. nebulosa* was never drilled ( $n = 12$ ).

#### Shell Thickness and Drilling Predation

When DF was compared against shell thickness, it showed strong, negative correlation (Spearman  $r_s = -0.599$ ,  $p = 0.024$ ). Species with thick shells were immune to drilling predation, while the average DF for thin shells was statistically significantly higher (0% versus 18.2%) (Table 7). Within thin species, average genus-level DF was highest for *Diplomeriza* (DF = 47.4%,  $n = 637$ ), followed by *Duplicaria* (DF = 28.8,  $n = 69$ ), *Myurella* (DF = 26.3%,  $n = 20$ ), *Impages* (DF = 12.5%,  $n = 45$ ), *Terebra* (DF = 10.5%,  $n = 38$ ) and *Hastula* (DF = 2.3%,  $n =$

172). Within *Terebra*, *T. sp.* had DF of 14.6 ( $n = 28$ ), whereas *T. tricolor* showed no evidence of drilling. Within *Hastula*, all two species showed variable DFs (*H. traillii* DF = 0.3%,  $n = 156$  and *H. tenera* DF = 18.8%,  $n = 16$ ).

#### Shell Slenderness and Drilling Predation

In the Indian subcontinent, family Terebridae comprised of 11 robust and three slender species (Table 8). Drilling frequency showed spectacular contrast between robust and slender species. While the robust species showed average DF of 13.2% ( $n = 885$ ), slender species were almost immune to drilling predation (DF = 0.1%,  $n = 194$ ). DF within 11 robust species varied from 0% to 47.4%, with the highest DF in *Diplomeriza spectabilis* (Table 8). Within three slender species, *Terebra commaculata* ( $n = 28$ ) and *T. tricolor* ( $n = 10$ ) showed no evidence of drilling (i.e., DF = 0%), and *H. traillii* had very low value of DF (0.3%,  $n = 156$ ).

#### Peeling Predation

##### Peeling Frequency (PF)

The overall PF in the family Terebridae from the Indian subcontinent showed an average value of 1.3 ( $n = 1,279$ ). In *Terebra*, PF was highest in *T. tricolor* (PF = 3.3,  $n = 10$ ), while *T. commaculata* and *T. sp.* both showed lower PF value of 1 ( $n = 40$  and  $n = 28$  respectively). In *Oxymeris*, genus-level average PF was 1.7 ( $n = 74$ ); species level PFs varied from 1.2 in *O. maculata* ( $n = 24$ ) to 2.3 in *O. crenulata* ( $n = 21$ ). In *Myurella*, PF was higher in *M. nebulosa* (PF = 1.1,  $n = 25$ ), and lower in *M. affinis* (PF = 0.9,  $n = 39$ ). Within genus *Hastula*, *H. traillii* showed higher PF value of 1 ( $n = 255$ ) whereas *H. tenera* had the lowest PF (0.4,  $n = 16$ ) not only within the genus but also within the entire studied family.

Peeling frequency varied greatly with size (Table 2). Within the family, the average PF for smaller specimens (i.e., < 4 cm) was 1.2 ( $n = 1007$ ), while the average PF for larger specimens (> 4 cm) was 2.3 ( $n = 102$ ) (Table 2). This was also true for the genus *Terebra*, *Myurella* and *Oxymeris*. In *Terebra*, smaller specimens showed PF of 1.5, while the larger specimens had higher PF (1.6). Similarly, in case of *Myurella*, PFs for the smaller and larger specimens were 1.2 and 1.8, respectively; also in case of *Oxymeris*, PF of smaller



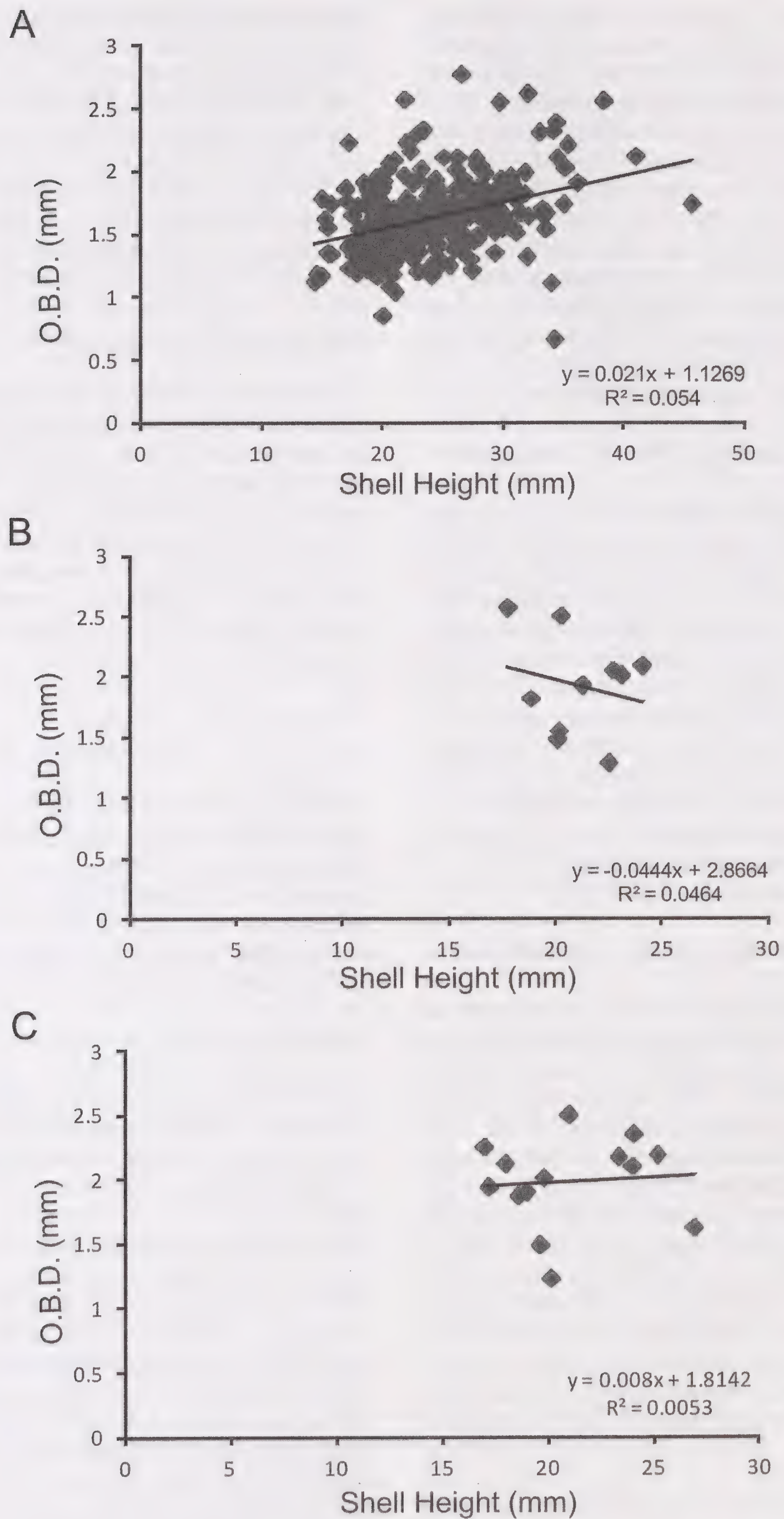


FIG. 4. Relationship between outer borehole diameter (OBD, proxy for predator size) of naticid drillholes and prey shell height of three abundant Indian terebrids. A: *Diplomeriza spectabilis*; B: *Myurella affinis*; C: *Duplicaria duplicata*. Note, in all cases, correlations were poor.



specimens was 1 while the larger specimens showed PF value of 1.8. However, for *Hastula*, *Diplomeriza*, *Duplicaria*, *Granuliterebra* and *Impages*, all specimens were smaller in size, and, therefore, such correlation could not be tested. All the specimens of *Diplomeriza spectabilis* were smaller in size, but had a large sample size ( $n = 637$ ). For this reason, we subdivided the specimens into three size classes (see Material and Methods). Still, PF increased with size (Table 3): PF was 0.5 in the smallest size class (10.1–20.0 mm), 0.8 for intermediate (20.1–30.0 mm) size class, and 1.7 in the larger size class ( $> 30$  mm).

#### Latitudinal Variability of Peeling Predation

For PF, the global dataset revealed an overall decreasing trend with increase in latitude (Table 4). However, similar to the DF studies, the total number of specimens was low from higher latitudes ( $> 50^\circ$ ). When all Indian subcontinental species were pooled together, a fluctuating trend across latitude was noticed (Table 5). This trend remained same even in case of the abundant species (Table 5). For these abundant species, PF was 0.9 ( $n = 44$ ) near the equator ( $0^\circ$ – $10^\circ$ ). However, in the next latitudinal bin ( $10^\circ$ – $20^\circ$ ), PF was highest (PF = 1.3,  $n = 497$ ), while in the highest latitudinal bin ( $20^\circ$ – $30^\circ$ ), PF declined to a value of 0.5 ( $n = 722$ ).

#### Shell Ornamentation and Peeling Predation

Peeling frequency decreases with increasing strength of ornamentation (Table 6). The average PF for the species with fine ornament (Category 1) was 1.6, whereas, in coarsely ornamented species (Category 2), PF was 0.9. Although the average PF on the strongly ornamented species was lower than that of the finely ornamented species, their difference was not statistically significant (t-test,  $p = 0.10$ ). In Category 2, PF was lowest (0.4) in *H. tenera* ( $n = 16$ ) and highest (2.3) in *O. crenulata* ( $n = 21$ ); whereas, in Category 1, the lowest PF was in both *T. commaculata* and *H. traillii* (PF = 1,  $n = 40$  and  $n = 255$  respectively), and the highest value of PF was in *T. tricolor* (PF = 3.3;  $n = 10$ ).

#### Shell Thickness and Peeling Predation

When PF was compared against shell thickness, it showed no correlation (Spearman  $r_s = 0.345$ ,  $p = 0.227$ ). Species with thick shells

(six species) showed average PF of 1.5, while, the average PF for thin-shelled species (eight species) was statistically not significantly lower (1.2) (Table 7). Within thin-shelled species, PF was highly variable, ranging from as high as 3.3 in *T. tricolor* to as low as 0.4 in *H. tenera* (Table 7). Similarly, for the thick-shelled species, PF varied from as low as 1 in *T. commaculata* to as high as 2.3 in *O. crenulata*. We did not have shell thickness data for *G. persica*.

#### Shell Slenderness and Peeling Predation

The average peeling frequency in robust species (11; Fig. 2) was 1 ( $n = 944$ ), while PF for the slender species (three; Fig. 2) was 1.8 ( $n = 305$ ) suggesting that these PFs were not statistically significantly different ( $p = 0.27$ ). PF within robust species varied from 0.4 in *H. tenera* to 2.3 in *O. crenulata*. In comparison, three slender species – *T. commaculata*, *H. traillii* – showed PF of 1, whereas *T. tricolor* showed PF of 3.3 (Table 8).

## DISCUSSION

Indian coastal waters harbour 77 terebrid species (Rao et al., 1991; Venkiteshaan & Mukherjee, 2012; only 32 species were repositied in ZSI, Kolkata). Out of these diverse species, we provided data on drilling and peeling predation for 15 abundant species ( $n \geq 10$ ) (Table 1).

#### Drilling Predation

Global as well as Indian drilling frequency on Recent terebrid gastropods is in general low compared to the modern global average of naticid drilling predation (Huntley & Kowalewski, 2007) (DF = 17%; see Vermeij et al., 1980, and their appendix 3) and 13.6% in India in particular (Table 1). DF varied spatially. In the Indo-West Pacific region, DF was 39.0%; however, it was based only on two species ( $n = 35$ ; Vermeij et al., 1980). India belongs to this Indo-West Pacific Biogeographic Province. When we inserted Indian, as well as other Indo-West Pacific data from our updated dataset, DF decreased to only 26.1% ( $n = 1,113$ ). Likewise, when eastern Pacific data from the ZSI samples were updated, DF decreased from 22.3% ( $n = 222$ ; Vermeij et al., 1980) to 17.9% ( $n = 1,308$ ; Appendix 1). However, we could not add up new data for the western Atlantic region



as the ZSI archive did not contain any specimen from this region, for which DF, estimated by Vermeij et al. (1980), was 6.3% ( $n = 196$ ). It now appears that DFs in different regions, as calculated by Vermeij et al. (1980), did not change significantly even when we added our new data to the global database. In the Indian subcontinent, the present day drilling predation on terebrids showed considerable variation at genus (DF ranges from 4.70% to 25.38%) as well as at species levels (DF ranges from 0% to 47.4%). The highest value of DF, which was found in *Diplomeriza spectabilis* ( $n = 637$ ), was also highest within the Indo-West Pacific Province. However, in Guam, *O. dimidiata* showed 70% DF (Vermeij et al., 1980). This high value in *O. dimidiata* may be due to small sample size ( $n = 10$ ).

High frequency of unsuccessful drilling is interpreted to indicate prey efficiency (PE). In Recent terebrid species PE values vary considerably. Low values were found for species which had high DF; for example, in *Diplomeriza spectabilis* DF was highest (47.4) and PE was lowest (0.04). Four species (*T. commaculata*, *O. crenulata*, *O. dimidiata* and *T. tricolor*) had high PE (= 1) and all showed no complete drillholes. Multiple drilling (MULT) was found only in one species, *Diplomeriza spectabilis* and its value was 0.3. As mentioned earlier multiple drillholes suggest imperfect prey handling by the predator. This would seem to conflict with high DF values and high stereotypy, which suggest high predator efficiency. Therefore, the high value of MULT in the present case cannot be explained by predator's imperfection theory. However, some workers reported that drilling predators, in a few cases, may drill an already drilled, dead individual, resulting in multiple drillholes on the prey (Hoffman et al., 1974; Stanton & Nelson, 1980; Pek & Mikulas, 1996). The present anomalous high value of MULT may be better explained by this observation (failure to recognise an empty shell may be another kind of inefficient or inept act of predation; Allmon, pers. comm., 2015).

DF showed a fluctuating pattern with latitudes if all global as well as all Indian species were pooled together (Tables 4, 5). However, when we considered only 15 abundant Indian species together, an increasing trend with latitude was observed (Table 5). For almost all latitudinal bins, DFs were very low, except for the 20°–30° latitudinal bin. Very high value of DF (46.9%;  $n = 722$ ) in this bin was mostly because of higher DF's in two species (*Diplomeriza spectabilis*

and *Duplicaria duplicata*) (Table 5). When these species were removed from the analysis, the average DF from this bin fell to 18.80%; ( $n = 16$ ), which was still the highest among all latitudinal bins (Table 5). The global pattern of DF observed in the terebrids was in sharp contrast with that observed in Recent turritelline gastropods, where the global DF decreased with increasing latitude (Paul et al., 2013).

Shell ornamentation is frequently thought to have a protective function against predation (Vermeij et al., 1980). For example, in turritelline gastropods, ornamentation seems to have deterred predation (Vermeij, 1978; Paul et al., 2013; but see Allmon et al., 1990). Although terebrid gastropods had axial elements which have been thought to offer protection from durophagy (Vermeij, 1982), we saw no such pattern in the case of drilling predation. Table 6 revealed that DF's were greater in ornamented species (Category 2) (for a similar observation: Signor 1985). We also demonstrated below that the same observation was made in the case of peeling predation. It is possible that for this clade, ornamentation might have evolved as a holdfast during burrowing (Signor, 1985). According to Vermeij (pers. comm., 2015), the range of sculpture in terebrids is not great enough to have any deterring effect on predation. Ornamentation simply may reflect different habitats where drilling predators may not have similar abundances.

Shell thickness has also been considered as an antipredatory adaptation (for similar observation: Paul et al., 2013). A statistically significant, negative correlation between shell thickness and DF (Spearman  $r_s = -0.62$ ,  $p = 0.018$ ) suggested an antipredatory role of thick shell. Terebrids with thinner apertural thickness were frequently drilled (DF = 18.2%), whereas species with thick shells were immune to drilling (DF = 0%) (Table 7). Because drilling in thick shell involves more time and energy, it might not be profitable to drill them, thus supporting the cost-benefit model (Kitchell et al., 1981; Mondal et al., 2010a). In one species (*Diplomeriza spectabilis*), we studied ontogenetic thickness changes. Thickness was maximum near the middle part of the shell where majority of the drillholes were located. Thickening of the shell in this stereotypic location may be an evolved morphological character.

Shell slenderness has been cited as having significant effect on predatory attack in other gastropods, for example, in the turritelline gas-



tropods (Zipser & Vermeij, 1978; Vermeij, 1981; Paul et al., 2013). However, for the terebrids, the relationship between shell slenderness and DF was not previously studied. Our results showed that the slender forms were less frequently drilled (DF = 0.10%) than the robust species (DF = 13.2%). Signor (1985) observed that slender terebrid shells had “low profile” (i.e., more slender) within their burrows and might evade detection by the epifaunal calappid crabs. We argue here that this shell slenderness was equally beneficial against detection by infaunal naticid drillers. On the contrary, robust shells were vulnerable to detection and fell as easy prey. Also slender shell might not be a profitable item for its small biomass.

The temporal record of naticid predation on terebrids is available since the Eocene. Drilling intensity during the Eocene was 11% ( $n = 53$ ), which was comparable with the present average value (17%; Appendix 1). From the Eocene, DF became higher in the Oligocene (39.5%,  $n = 58$ ), and remained high in the Miocene (32.4%,  $n = 525$ ). However, DF declined during the Pliocene (16.6%,  $n = 133$ ) and Pleistocene (10.6%,  $n = 100$ ), and approached modern values. Temporally declining (since Miocene) low values may be explained by the antipredatory adaptation of the terebrid gastropods with time. In fact, Vermeij et al. (1980) observed that increase of body size in Recent terebrid species took place as a response to resist naticid drilling predation. We, here, also noted that large species were almost immune to naticid drilling predation (Table 2). Moreover, terebrid gastropods may also have adapted to antipredatory behaviour (for such evolutionary change of turritelline gastropods: Paul et al., 2013). Recent terebrids are efficient burrowers (Signor, 1985), which perhaps help them to protect from predation. Moreover, presence of toxins (called teretoxin; Puillandre & Holford, 2010), may be another reason why recent terebrids have low predation intensity, although we don't know about the use of this toxin as a deterrent of predation. If so, then this might make the story of shell form as selected for protection much more complicated (Allmon, pers. comm., 2015). Site stereotypy of the three abundant Indian species speaks for predators' adaptation for efficient drilling (Fig. 3). Stereotypy occurred at the middle part of the shell height, which suggested that terebrids could retract their soft parts well inside the shells (up to 50% of the shell height from the apex). We were not aware of such stereotypy in fossil terebrids.

### Peeling Predation

Table 1 listed peeling frequency of the family as a whole as well as PFs at the lower taxon-levels for the Indian subcontinent. Family level data were higher (for species  $n \geq 10$ , PF = 1.3,  $n = 1,279$ ) than values in individual biogeographic provinces shown by Vermeij et al. (1980). India belongs to the Indo-West Pacific biogeographic region where Vermeij et al. (1980) documented the highest PF (0.96). But the average value of PF (1.3) for the Indian species was even higher than the average Indo-West Pacific value (Table 1). At species level, Indian terebrids showed considerable variations, ranging from 0.38 in *Hastula tenera* to 3.3 in *Terebra tricolor* (Table 1).

For all global species pulled together, PF showed an overall decreasing trend with increasing latitude (Table 4). In contrast, when only the Indian species were considered, PF demonstrated fluctuating pattern with the highest PF at the 10°–20° latitudinal bin; the same pattern is also evident when only the abundant species were studied together (Table 5). High value of PF in this bin cannot be attributed to the total number of specimens. Although in the 20°–30° bin, sample was highest ( $n = 722$ ), PF was lowest in this bin (0.52; Table 5). The global pattern of decreasing PF with increasing latitude was also recorded for Recent turritelline gastropods (Paul et al., 2013).

Peeling frequency increased with increasing body size (Table 2). According to Vermeij et al. (1980), larger shells were likely to have sustained more non-lethal attacks and therefore had higher PF values. Similar observation was made by many other workers for the turritelline gastropods (Miller, 1975; Zipser & Vermeij, 1978; Vermeij & Dudley, 1982; Allmon et al., 1990; Paul et al., 2013; but see Kabat & Kohn, 1986). Even within a species, relatively lower values of PF were shown by young specimens of larger species (e.g., *Terebra tricolor*). The low value of PF in smaller species can be explained either by the energy maximization model where smaller species were energetically not profitable (Kitchell et al., 1980), or due to their ecological behaviour. Similar observation of low predation intensity on smaller size class was made by Waite & Strasser (2011) in turritelline gastropods. They argued that the low PF might be due to the fact that they lived predominantly infaunally and thus escaped the notice of epifaunal crabs (see also Campbell & Fielder, 1986).



Although we expected that the species with greater apertural thickness should have lower peeling frequency, no such correlation was revealed from our study (Table 7). Ornaments in terebrid gastropods are mainly axial and some are nodose (Fig. 2). We expected that these features were deterrent to breakage and could increase the chances of more sublethal attacks thereby raising the value of PF. But our comparison between shell ornamentation and PF did not support such expectation (Table 6). Smooth shells showed higher PF value than ornamented species. However, close study revealed that these anomalous PF values resulted from the shell size of the species. Highly ornamented larger species (*Oxymeris crenulata*, *Myurella nebulosa*) had high PF values. Even their PF values were greater than larger species of smooth taxa (*O. dimidiata*, *T. subulata*). Lack of correlation between peeling frequency and the external ornamentation as well as shell thickness may also be explained by the limitation of PF as measure of predation intensity (see also Signor, 1985). Two recent studies on shell breaking predation have documented that, interpretation based on PF alone may be faulty, use of both the failed (as identified by repaired scars) and successful attack (identified by unrepaired shell breaks) components of predation in tandem are more reliable to better constrain potential paleoecological interpretations (Mondal et al., 2014b; Mondal & Harries, 2015).

Shell slenderness might also affect peeling predation and some workers believed that there is a positive correlation between shell slenderness and PF (Vermeij et al., 1980). But while this was tested in the terebrid family by Signor (1985), no significant difference emerged. In our data the PF values were 1 and 1.8 for “robust” and “slender” forms respectively, suggesting that PF for the slender species was statistically not significantly different than that for the robust species (t-test,  $p = 0.27$ ). Both Vermeij et al. (1980) and Signor (1985) performed their analyses on the basis of small specimens (< 4 cm). Out of our three abundant slender species, one was “large” (*Terebra commaculata*) and another (*Hastula traillii*) was “small”; the third one (*Terebra tricolor*) had both size classes. And among robust group, four out of 11 species were large (> 4 cm), and six species were small (< 4 cm) (Table 2). The other species (*O. maculata*), had both small and large individuals (Table 2). Within the “robust” class, PF was greater in larger species (1.91), which was significantly higher ( $p = 0.002$ ) than PF in smaller species (0.87). While we compared

PFs of our smaller, robust species (PF = 0.87) with those of Vermeij et al. (1980) and Signor (1985) differences were not significant (PF = 0.64 in Signor (1985), and 0.55 in Vermeij et al. (1980). It appeared therefore that the size of the prey was more of a deterrent than shell shape against peeling predation.

## CONCLUSIONS

- (1) Drilling and shell-breaking predation on the Recent Indian subcontinental terebrid species were studied based on a newly updated, global database. The database was based on a huge collection in the ZSI, Kolkata; our own collections from the eastern and western coasts of India; and previously published literature.
- (2) Recent abundant (i.e.,  $n \geq 10$ ) Indian terebrids had drilling frequency (DF) of 13.6% which showed considerable variation at lower-taxon levels. DF increased with increasing latitude. Naticid gastropods were evolved as evident from the stereotypy of the drillhole site (i.e., second to third whorl from aperture), but size stereotypy showed poor correlation.
- (3) Peeling frequency (PF) in abundant terebrids from India was the highest in the world. Genus- and species-level PFs displayed considerable variation. PF varied with latitude, but no trend was established.
- (4) Comparison between present Indian data and revised global database revealed that low value of DF in Indian terebrids was consistent with global data. Temporally, DF showed fluctuating trend, but today's terebrids were escalated.
- (5) The overall pattern of drilling and shell-breaking predation on the members of the family Terebridae, suggested that external shell ornamentation and shell thickness did not play any significant role, whereas shell shape had weak effect in deterring predation. However, shell size played an antipredatory role in minimizing the overall intensity of drilling and shell-peeling predation. Along with behavioural adaptations (i.e., infaunalization and toxin to deter predation), these antipredatory morphological characters helped Recent terebrid gastropods to minimize predation.



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APPENDIX

New global dataset of drilling and peeling predation on Recent terebrid gastropods (n = number of specimens; DF = Drilling Frequency, PF = Peeling Frequency).

| Species/Locality                     | n   | DF (%) | PF   | Reference            |
|--------------------------------------|-----|--------|------|----------------------|
| <i>Cinguloterebra</i>                |     |        |      |                      |
| <i>C. anilis</i> (Röding, 1798)      |     |        |      |                      |
| Unknown                              | 1   | 0      | 1.00 | Present Study        |
| Mergui Island                        | 1   | 0      | 1.00 | Present Study        |
| Unknown                              | 2   | 0      | 2.00 | Present Study        |
| Wom Village, Papua New Guinea        | 10  | -      | 1.10 | Vermeij et al., 1980 |
| Ambatoloaka, Madagascar              | 53  | -      | 1.00 | Vermeij et al., 1980 |
| Nosy Iranja, Madagascar              | 19  | -      | 0.53 | Vermeij et al., 1980 |
| North of Cairns, Queensland          | 29  | -      | 0.81 | Vermeij et al., 1980 |
| <i>Duplicaria</i>                    |     |        |      |                      |
| <i>D. dussumierii</i> (Kiener, 1839) |     |        |      |                      |
| Madagascar                           | 2   | 0      | 1.00 | Present Study        |
| <i>D. australis</i> (Smith, 1873)    |     |        |      |                      |
| Darwin, Australia                    | 23  | 43     | 0.74 | Vermeij et al., 1980 |
| Sydney, New South Wales              | 16  | -      | 0.88 | Vermeij et al., 1980 |
| <i>D. duplicata</i> (Linnaeus, 1758) |     |        |      |                      |
| Mandvi, Gujarat                      | 63  | 28.8   | 0.50 | Present Study        |
| Chu Lai, Vietnam                     | 12  | 17     | 1.50 | Vermeij et al., 1980 |
| Andaman                              | 6   | 0      | 1.00 | Present Study        |
| Unknown                              | 13  | 31     | 1.60 | Present Study        |
| <i>D. ustulata</i> (Deshayes, 1857)  |     |        |      |                      |
| Richmond, Victoria                   | 10  | -      | 0.40 | Vermeij et al., 1980 |
| <i>Diplomeriza</i>                   |     |        |      |                      |
| <i>D. fietilis</i> Hinds, 1844       |     |        |      |                      |
| Durban Bay                           | 2   | 0      | 0.50 | Present Study        |
| <i>D. spectabilis</i> Hinds, 1844    |     |        |      |                      |
| Chandipur 2011                       | 76  | 52.6   | 0.75 | Present Study        |
| Chandipur 2012                       | 561 | 50.1   | 0.85 | Present Study        |
| <i>Euterebra</i>                     |     |        |      |                      |
| <i>E. tristis</i> (Deshayes, 1859)   |     |        |      |                      |
| Wellington, New Zealand              | 10  | -      | 0.60 | Vermeij et al., 1980 |
| Auckland, New Zealand                | 10  | -      | 0.30 | Vermeij et al., 1980 |
| Cook Straits, New Zealand            | 22  | -      | 0.27 | Vermeij et al., 1980 |
| Port Jackson, New South Wales        | 22  | -      | 0.27 | Vermeij et al., 1980 |
| Cronulla, New South Wales            | 29  | -      | 0.10 | Vermeij et al., 1980 |
| <i>E. assecla</i> (Iredale, 1924)    |     |        |      |                      |
| Twofold Bay, New South Wales         | 11  | -      | 0.18 | Vermeij et al., 1980 |
| Montague Island, New South Wales     | 21  | -      | 0.33 | Vermeij et al., 1980 |

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(continued)

| Species/Locality                      | n   | DF (%) | PF   | Reference            |
|---------------------------------------|-----|--------|------|----------------------|
| <i>E. capensis</i> (Smith, 1873)      |     |        |      |                      |
| Capetown, South Africa                | 11  | -      | 0.27 | Vermeij et al., 1980 |
| <i>Granuliterebra</i>                 |     |        |      |                      |
| <i>G. persica</i> (Smith, 1877)       |     |        |      |                      |
| Madras, India                         | 30  | -      | 0.78 | Vermeij et al., 1980 |
| <i>Hastula</i>                        |     |        |      |                      |
| <i>H. albula</i> (Menke, 1843)        |     |        |      |                      |
| Andaman                               | 4   | 25     | 0.75 | Present Study        |
| Unknown                               | 6   | 0      | 0.50 | Present Study        |
| Durban Bay                            | 1   | 0      | 2.00 | Present Study        |
| <i>H. hectic</i> (Linnaeus, 1758)     |     |        |      |                      |
| Seychelles                            | 2   | 0      | 0    | Present Study        |
| Ceylon                                | 1   | 0      | 5.00 | Present Study        |
| Unknown                               | 8   | 0      | 2.25 | Present Study        |
| Lubang, Mindoro                       | 11  | -      | 0.73 | Vermeij et al., 1980 |
| Nosy-Be, Madagascar                   | 16  | -      | 2.06 | Vermeij et al., 1980 |
| Nosy-Be                               | 104 | -      | 1.62 | Vermeij et al., 1980 |
| Bougainville, Solomons                | 60  | -      | 0.33 | Vermeij et al., 1980 |
| Mogadishu, Somalia                    | 10  | -      | 0.50 | Vermeij et al., 1980 |
| Point venus, Tahiti                   | 58  | -      | 1.27 | Vermeij et al., 1980 |
| Ahonu River, Tahiti                   | 87  | -      | 0.85 | Vermeij et al., 1980 |
| Papeete, Tahiti                       | 20  | -      | 0.10 | Vermeij et al., 1980 |
| Unknown                               | 37  | 0      | 1.19 | Present Study        |
| India                                 | 4   | 0      | 0.50 | Present Study        |
| Singapore                             | 2   | 0      | 0.50 | Present Study        |
| <i>H. exacuminata</i> Sacco, 1891     |     |        |      |                      |
| South Africa                          | 2   | 0      | 1.50 | Present Study        |
| <i>H. lanceata</i> (Linnaeus, 1767)   |     |        |      |                      |
| Ascension                             | 2   | 0      | 3.00 | Present Study        |
| Aldabra                               | 19  | -      | 0.37 | Vermeij et al., 1980 |
| Mauritios                             | 2   | 0      | 1.50 | Present Study        |
| <i>H. brazier</i> (Angas, 1871)       |     |        |      |                      |
| Pt. Stephens                          | 2   | 0      | 2.00 | Present Study        |
| <i>H. penicillata</i> (Hinds, 1844)   |     |        |      |                      |
| Bourbon                               | 5   | 0      | 1.00 | Present Study        |
| Easter Island                         | 10  | -      | 0.30 | Vermeij et al., 1980 |
| <i>H. solida</i> (Deshayes, 1857)     |     |        |      |                      |
| Borongan, Samar                       | 24  | -      | 1.25 | Vermeij et al., 1980 |
| <i>H. strigilata</i> (Linnaeus, 1758) |     |        |      |                      |
| Honolulu, Oahu                        | 42  | -      | 1.31 | Vermeij et al., 1980 |
| Koeta, Bali                           | 52  | -      | 1.23 | Vermeij et al., 1980 |
| Calapan, Mindoro                      | 18  | -      | 0.72 | Vermeij et al., 1980 |

(continues)



(continued)

| Species/Locality                        | n   | DF (%) | PF   | Reference            |
|-----------------------------------------|-----|--------|------|----------------------|
| <i>H. hastata</i> (Gmelin, 1791)        |     |        |      |                      |
| Alicetown, Bahamas                      | 12  | -      | 1.42 | Vermeij et al., 1980 |
| Abaco, Bahamas                          | 10  | -      | 1.30 | Vermeij et al., 1980 |
| Grand Cayman                            | 14  | -      | 1.00 | Vermeij et al., 1980 |
| St Thomas                               | 11  | -      | 0.73 | Vermeij et al., 1980 |
| Pine Key, West Indies                   | 14  | -      | 0.71 | Vermeij et al., 1980 |
| Great Inagua, Bahamas                   | 12  | -      | 0.58 | Vermeij et al., 1980 |
| Bimini, Bahamas                         | 22  | -      | 0.45 | Vermeij et al., 1980 |
| Unknown                                 | 5   | 0      | 1.60 | Present Study        |
| <i>H. aciculina</i> (Lamarck, 1822)     |     |        |      |                      |
| Cape palmas, Liberia                    | 21  | -      | 0.43 | Vermeij et al., 1980 |
| Banana, Zaire                           | 68  | -      | 0.25 | Vermeij et al., 1980 |
| Lumley Beach, Sierre Leone              | 12  | -      | 0.25 | Vermeij et al., 1980 |
| Johnobe, Sierre Leone                   | 12  | -      | 0.08 | Vermeij et al., 1980 |
| Lagos, Nigeria                          | 22  | -      | 0    | Vermeij et al., 1980 |
| Australia                               | 4   | 0      | 0.50 | Present Study        |
| Ceylon                                  | 5   | 60     | 1.40 | Present Study        |
| <i>H. tenera</i> (Hinds, 1844)          |     |        |      |                      |
| Bombay                                  | 16  | 18.8   | 0.38 | Present Study        |
| Singapore                               | 8   | 12.5   | 0.63 | Present Study        |
| Oman                                    | 10  | 10     | 0.30 | Present Study        |
| <i>H. traillii</i> Deshayes, 1859       |     |        |      |                      |
| Gopalpur, India                         | 38  | 0      | 1.50 | Present Study        |
| Puri, India                             | 11  | 0      | 1.09 | Present Study        |
| Vizagapatnam                            | 107 | 0.93   | 2.02 | Present Study        |
| <i>H. sp.</i>                           |     |        |      |                      |
| Unknown                                 | 3   | 66.7   | 1.33 | Present Study        |
| <i>H. cuspidata</i> (Hinds, 1844)       |     |        |      |                      |
| West Africa                             | 2   | 0      | 1.00 | Present Study        |
| <i>H. laurina</i> Hinds, 1844           |     |        |      |                      |
| Marquesas                               | 2   | 0      | 1.00 | Present Study        |
| Ceylon                                  | 3   | 0+2    | 1.67 | Present Study        |
| Unknown                                 | 1   | 0      | 5.00 | Present Study        |
| <i>H. matheroniana</i> (Deshayes, 1859) |     |        |      |                      |
| Unknown                                 | 3   | 33     | 1.33 | Present Study        |
| Ceylon                                  | 8   | 38     | 0.25 | Present Study        |
| <i>H. inconstans</i> (Hinds, 1844)      |     |        |      |                      |
| Marguis Island                          | 2   | 0      | 0.50 | Present Study        |
| Marquesas                               | 16  | 6.25   | 0.88 | Present Study        |
| Sandwon Island                          | 1   | 0      | 0    | Present Study        |
| Unknown                                 | 2   | 0      | 0.50 | Present Study        |
| Andaman                                 | 4   | 0      | 2.25 | Present Study        |

(continues)



(continued)

| Species/Locality                    | n  | DF (%) | PF   | Reference            |
|-------------------------------------|----|--------|------|----------------------|
| <i>H. sp.</i>                       |    |        |      |                      |
| Unknown                             | 3  | 0+1    | 2.67 | Present Study        |
| <i>Hastulopsis</i>                  |    |        |      |                      |
| <i>H. conspersa</i> (Hinds, 1844)   |    |        |      |                      |
| Motupore Island, Papua New Guinea   | 21 | -      | 1.10 | Signor, 1985         |
| <i>H. alveolata</i> (Hinds, 1844)   |    |        |      |                      |
| Unknown                             | 2  | 50     | 1.50 | Present Study        |
| <i>Impages</i>                      |    |        |      |                      |
| <i>I. stylata</i> (Hinds, 1844)     |    |        |      |                      |
| Indian Ocean                        | 2  | 0      | 0    | Present Study        |
| Unknown                             | 6  | 16.7   | 0.67 | Present Study        |
| Papeete, Tahiti                     | 16 | -      | 0.94 | Vermeij et al., 1980 |
| Marguilis Island                    | 6  | 0      | 0.67 | Present Study        |
| <i>I. nassoides</i> (Hinds, 1844)   |    |        |      |                      |
| Unknown                             | 2  | 50     | 0.50 | Present Study        |
| Ceylon                              | 7  | 42.9   | 0.57 | Present Study        |
| <i>I. anomala</i> (Gray, 1834)      |    |        |      |                      |
| Mergui Island                       | 5  | 40     | 0.40 | Present Study        |
| <i>I. bacillus</i> (Deshayes, 1859) |    |        |      |                      |
| Tjilatjap, Java                     | 23 | -      | 0.35 | Vermeij et al., 1980 |
| Gopalpur                            | 4  | 25     | 1.25 | Present Study        |
| Bilipatam                           | 41 | 0      | 1.54 | Present Study        |
| <i>I. cinerea</i> (Born, 1778)      |    |        |      |                      |
| Saint Thomas                        | 37 | -      | 0.95 | Vermeij et al., 1980 |
| Areia Branca, Brazil                | 14 | -      | 0.71 | Vermeij et al., 1980 |
| Recife, Brazil                      | 14 | -      | 0.71 | Vermeij et al., 1980 |
| Trinidad                            | 68 | -      | 0.63 | Vermeij et al., 1980 |
| Olinda, Pernambuco, Brazil          | 10 | -      | 0.60 | Vermeij et al., 1980 |
| Jupiter Inlet, Florida              | 16 | -      | 0.56 | Vermeij et al., 1980 |
| Barbados                            | 56 | -      | 0.52 | Vermeij et al., 1980 |
| Itanhaena, Santos, Brazil           | 17 | -      | 0    | Vermeij et al., 1980 |
| Mazatlan, Mexico                    | 12 | -      | 0.83 | Vermeij et al., 1980 |
| San Jose, Perlas, Panama            | 23 | -      | 0.78 | Vermeij et al., 1980 |
| Puerto Culebra, Costa Rica          | 11 | -      | 0.64 | Vermeij et al., 1980 |
| <i>I. maryleeae</i> (Burch, 1965)   |    |        |      |                      |
| Texas                               | 11 | -      | 1.18 | Vermeij et al., 1980 |
| Mustang Island, Texas               | 17 | -      | 0.41 | Vermeij et al., 1980 |
| Mujeres Island, Quintana Roo        | 12 | -      | 0    | Vermeij et al., 1980 |
| <i>I. salleana</i> (Deshayes, 1859) |    |        |      |                      |
| Panama City, Florida                | 10 | -      | 0.50 | Vermeij et al., 1980 |
| Gulf Park, Alabama                  | 25 | -      | 0.32 | Vermeij et al., 1980 |
| Aransas Island, Texas               | 30 | -      | 0.30 | Vermeij et al., 1980 |

(continues)



(continued)

| Species/Locality                           | n   | DF (%) | PF   | Reference            |
|--------------------------------------------|-----|--------|------|----------------------|
| <i>Myurella</i>                            |     |        |      |                      |
| <i>M. affinis</i> (Gray, 1834)             |     |        |      |                      |
| Sandwich Island                            | 4   | 0      | 1.25 | Present Study        |
| Kavaratti, Laksadurga                      | 1   | 0      | 1.00 | Present Study        |
| Scyelles                                   | 3   | 0      | 4.67 | Present Study        |
| Lubang Island (Mindoro)                    | 6   | 0      | 2.67 | Present Study        |
| Unknown                                    | 5   | 0      | 1.00 | Present Study        |
| Andaman                                    | 19  | 52.6   | 1.42 | Present Study        |
| Calapan, Mindoro                           | 12  | -      | 2.58 | Vermeij et al., 1980 |
| Batangas, Luzon                            | 11  | -      | 2.55 | Vermeij et al., 1980 |
| Kandavu, Fiji                              | 16  | -      | 2.19 | Vermeij et al., 1980 |
| Imbu, Okinawa                              | 39  | -      | 1.78 | Vermeij et al., 1980 |
| Nadi, Fiji                                 | 65  | -      | 1.63 | Vermeij et al., 1980 |
| Okinawa                                    | 161 | -      | 1.63 | Vermeij et al., 1980 |
| East Channel, Aldabra                      | 10  | -      | 1.5  | Vermeij et al., 1980 |
| Green Island, Queensland                   | 13  | -      | 1.39 | Vermeij et al., 1980 |
| Tumon Bay, Guam                            | 21  | -      | 1.38 | Vermeij et al., 1980 |
| Losap, Mortlock Island                     | 59  | -      | 1.19 | Vermeij et al., 1980 |
| Pange, Zanzibar                            | 20  | -      | 1.19 | Vermeij et al., 1980 |
| Passe Femme, Aldabra                       | 23  | -      | 1.04 | Vermeij et al., 1980 |
| Alfons, Almirantes Island                  | 65  | -      | 0.95 | Vermeij et al., 1980 |
| Auraupushekaru, Palau                      | 20  | -      | 0.95 | Vermeij et al., 1980 |
| Muti, Enewetak                             | 15  | -      | 0.87 | Vermeij et al., 1980 |
| Passe Guionnet, Aldabra                    | 27  | -      | 0.85 | Vermeij et al., 1980 |
| Opunohu Bay, Guam                          | 15  | -      | 0.67 | Vermeij et al., 1980 |
| Imrodj, Jaluit Atoll                       | 54  | -      | 0.59 | Vermeij et al., 1980 |
| Pago Bay, Guam                             | 30  | -      | 0.50 | Vermeij et al., 1980 |
| Avapahi, Huahine                           | 25  | -      | 0.40 | Vermeij et al., 1980 |
| Passe Guionnet, Aldabra                    | 34  | -      | 0.39 | Vermeij et al., 1980 |
| Addu Atoll, Maldives                       | 19  | -      | 0.37 | Vermeij et al., 1980 |
| Kiwengwa, Zanzibar                         | 58  | -      | 0.31 | Vermeij et al., 1980 |
| Kagi Island, Male Atoll                    | 43  | -      | 0.23 | Vermeij et al., 1980 |
| Addu Atoll                                 | 22  | -      | 0.18 | Vermeij et al., 1980 |
| Pago Bay, Guam                             | 53  | 19     | -    | Vermeij et al., 1980 |
| Motupore Island, Papua New Guinea          | 12  | -      | 1.33 | Signor, 1985         |
| Honolulu                                   | 2   | 0      | 0.50 | Present Study        |
| <i>M. nebulosa</i> (G. B. Sowerby I, 1825) |     |        |      |                      |
| Andaman                                    | 12  | 0      | 1.83 | Present Study        |
| Port Blair, Andaman                        | 13  | -      | 0.39 | Vermeij et al., 1980 |
| <i>M. undulata</i> (Gray, 1834)            |     |        |      |                      |
| Unknown                                    | 1   | 0      | 0    | Present Study        |
| Australia                                  | 1   | 0      | 0    | Present Study        |
| Waikiki, Oahu                              | 14  | -      | 0.57 | Vermeij et al., 1980 |

(continues)



(continued)

| Species/Locality                     | n  | DF (%) | PF   | Reference            |
|--------------------------------------|----|--------|------|----------------------|
| Bougainville, Solomons               | 38 | -      | 0.53 | Vermeij et al., 1980 |
| New Britain                          | 23 | -      | 0.26 | Vermeij et al., 1980 |
| Motupore island, Papua New Guinea    | 24 | -      | 0.58 | Signor, 1985         |
| <i>M. columellaris</i> (Hinds, 1844) |    |        |      |                      |
| Honolulu, Oahu                       | 38 | -      | 0.61 | Vermeij et al., 1980 |
| Port Blair, Andaman                  | 14 | -      | 0.43 | Vermeij et al., 1980 |
| Rabaul, New Britain                  | 98 | -      | 0.24 | Vermeij et al., 1980 |
| Motupore Island, Papua New Guinea    | 45 | -      | 0.76 | Signor, 1985         |
| <i>M. kilburni</i> (Burch, 1965)     |    |        |      |                      |
| Motupore Island, Papua New Guinea    | 36 | -      | 0.80 | Signor, 1985         |
| <i>Oxymeris</i>                      |    |        |      |                      |
| <i>O. dimidiata</i> (Linnaeus, 1758) |    |        |      |                      |
| Andaman                              | 13 | 0      | 2.23 | Present Study        |
| Singapore                            | 4  | 0      | 3.75 | Present Study        |
| Unknown                              | 5  | 0      | 3.00 | Present Study        |
| Onna, Okinawa                        | 15 | -      | 2.47 | Vermeij et al., 1980 |
| Calatagan, Luzon                     | 10 | -      | 1.70 | Vermeij et al., 1980 |
| Raiatea                              | 15 | -      | 1.53 | Vermeij et al., 1980 |
| Port Blair, Andaman                  | 16 | -      | 1.19 | Vermeij et al., 1980 |
| Calapan, Mindoro                     | 20 | -      | 0.92 | Vermeij et al., 1980 |
| Losap, Mortlock Island               | 21 | -      | 0.90 | Vermeij et al., 1980 |
| Geelvink Bay, Iran Jaya              | 17 | -      | 0.88 | Vermeij et al., 1980 |
| Pogo Bay, Guam                       | 47 | -      | 0.47 | Vermeij et al., 1980 |
| Pago Bay, Guam                       | 10 | 70     | -    | Vermeij et al., 1980 |
| Motupore Island, Papua New Guinea    | 4  | -      | 0    | Signor, 1985         |
| <i>O. crenulata</i> (Linnaeus, 1758) |    |        |      |                      |
| Andaman                              | 21 | 0      | 2.29 | Present Study        |
| Station-628                          | 2  | 0      | 2.50 | Present Study        |
| North of Root Land                   | 4  | 25     | 1.25 | Present Study        |
| Nadi, Fiji                           | 54 | -      | 1.71 | Vermeij et al., 1980 |
| Susu Roso, Solomons                  | 12 | -      | 1.42 | Vermeij et al., 1980 |
| Honokowai, Maui                      | 11 | -      | 1.27 | Vermeij et al., 1980 |
| Mushu, Papua New Guinea              | 10 | -      | 1.00 | Vermeij et al., 1980 |
| Nukuhiva, Marquesas                  | 10 | -      | 0.80 | Vermeij et al., 1980 |
| Maui                                 | 33 | -      | 0.67 | Vermeij et al., 1980 |
| Pago Bay, Guam                       | 91 | -      | 0.30 | Vermeij et al., 1980 |
| <i>O. maculata</i> (Linnaeus, 1758)  |    |        |      |                      |
| Singapore & Maldives                 | 12 | 0      | 2.00 | Present Study        |
| Mindora                              | 1  | 0      | 1.00 | Present Study        |
| Lakshadweep                          | 1  | 0      | 0    | Present Study        |
| Unknown                              | 1  | 0      | 2.00 | Present Study        |
| Mokapu, Oahu                         | 12 | -      | 3.25 | Vermeij et al., 1980 |

(continues)



(continued)

| Species/Locality                    | n  | DF (%) | PF   | Reference            |
|-------------------------------------|----|--------|------|----------------------|
| Gomumu, Obi, Moluccas               | 13 | -      | 1.85 | Vermeij et al., 1980 |
| Wandamen Bay, Irian Jaya            | 15 | -      | 1.53 | Vermeij et al., 1980 |
| Savaii, Samoa                       | 24 | -      | 1.50 | Vermeij et al., 1980 |
| Honolulu, Oahu                      | 17 | -      | 1.47 | Vermeij et al., 1980 |
| Dunidu, Addu Atoll                  | 11 | -      | 1.45 | Vermeij et al., 1980 |
| Maui                                | 42 | -      | 1.20 | Vermeij et al., 1980 |
| Duke of Yourk Island                | 14 | -      | 1.21 | Vermeij et al., 1980 |
| Borongan, Samar                     | 23 | -      | 1.00 | Vermeij et al., 1980 |
| Chumbe, Zanzibar                    | 13 | -      | 1.00 | Vermeij et al., 1980 |
| Mataeia                             | 10 | -      | 1.00 | Vermeij et al., 1980 |
| Palau                               | 16 | -      | 0.56 | Vermeij et al., 1980 |
| <i>O. felina</i> (Dillwyn, 1817)    |    |        |      |                      |
| Lakshadweep                         | 2  | 0      | 2.00 | Present Study        |
| Seychelles                          | 3  | 33.3   | 1.00 | Present Study        |
| Deago garciaes                      | 2  | 50     | 1.50 | Present Study        |
| Imbu, Okinawa                       | 15 | -      | 2.73 | Vermeij et al., 1980 |
| Zanzibar                            | 18 | -      | 1.83 | Vermeij et al., 1980 |
| Honolulu, Oahu                      | 15 | -      | 1.53 | Vermeij et al., 1980 |
| Kaanapali, Maui                     | 11 | -      | 1.36 | Vermeij et al., 1980 |
| Kiwengwa, Zanzibar                  | 47 | -      | 0.51 | Vermeij et al., 1980 |
| Cocos-keeling Atoll                 | 14 | -      | 0.14 | Vermeij et al., 1980 |
| Muti, Enewetak                      | 17 | -      | 0.12 | Vermeij et al., 1980 |
| Kings Mill                          | 2  | 0      | 1.50 | Present Study        |
| <i>O. cerithina</i> (Lamarck, 1822) |    |        |      |                      |
| Maldives                            | 1  | 0      | 0    | Present Study        |
| Seychelles                          | 3  | 0      | 1.66 | Present Study        |
| Unknown                             | 7  | 0      | 2.00 | Present Study        |
| Moutobini, Tahiti                   | 14 | -      | 3.93 | Vermeij et al., 1980 |
| Onna, Okinawa                       | 24 | -      | 2.58 | Vermeij et al., 1980 |
| Ngeyangel, Palau                    | 26 | -      | 1.06 | Vermeij et al., 1980 |
| Nadi, Fiji                          | 14 | -      | 0.93 | Vermeij et al., 1980 |
| Palau                               | 10 | -      | 0.50 | Vermeij et al., 1980 |
| Enewetak Atoll                      | 18 | -      | 0.39 | Vermeij et al., 1980 |
| Honolulu, Oahu                      | 42 | -      | 0.43 | Vermeij et al., 1980 |
| <i>O. areolata</i> (Link, 1807)     |    |        |      |                      |
| Calapan, Mindoro                    | 38 | -      | 1.50 | Vermeij et al., 1980 |
| Honolulu, Oahu                      | 10 | -      | 1.00 | Vermeij et al., 1980 |
| New Caledonia                       | 10 | -      | 0.70 | Vermeij et al., 1980 |
| Alfons, Almirantes Island           | 16 | -      | 0.44 | Vermeij et al., 1980 |
| Motupore Island, Papua New Guinea   | 9  | -      | 0.33 | Signor, 1985         |
| <i>O. chlorata</i> (Lamarck, 1822)  |    |        |      |                      |
| Ngeyangel, Palau                    | 11 | -      | 1.64 | Vermeij et al., 1980 |
| Honolulu, Oahu                      | 14 | -      | 1.57 | Vermeij et al., 1980 |
| Kaanapali, Maui                     | 11 | -      | 1.00 | Vermeij et al., 1980 |

(continues)



(continued)

| Species/Locality                           | n  | DF (%) | PF   | Reference            |
|--------------------------------------------|----|--------|------|----------------------|
| <i>O. gouldi</i> (Deshayes, 1857)          |    |        |      |                      |
| Pease collection, Hawaii                   | 16 | -      | 9.19 | Vermeij et al., 1980 |
| Maui                                       | 20 | -      | 1.85 | Vermeij et al., 1980 |
| Honolulu, Oahu                             | 67 | -      | 0.63 | Vermeij et al., 1980 |
| <i>O. strigata</i> (G. B. Sowerby I, 1825) |    |        |      |                      |
| Venado Beach, Panama                       | 10 | 4.00   | 1.00 | Vermeij et al., 1980 |
| <i>O. senegalensis</i> (Lamarck, 1822)     |    |        |      |                      |
| C. B. Adams Collection                     | 10 | -      | 1.20 | Vermeij et al., 1980 |
| Senegal                                    | 11 | -      | 0.55 | Vermeij et al., 1980 |
| <i>O. albida</i> (Gray, 1834)              |    |        |      |                      |
| Westernport, Victoria                      | 17 | -      | 0.96 | Vermeij et al., 1980 |
| <i>Pristiterebra</i>                       |    |        |      |                      |
| <i>P. tuberculosa</i> (Hinds, 1844)        |    |        |      |                      |
| Venado Beach, Panama                       | 14 | 14     | 0.50 | Vermeij et al., 1980 |
| Farfan Beach, Panama                       | 98 | 12.24  | 0.35 | Vermeij et al., 1980 |
| Fort Amador, Panama                        | 24 | -      | 0.25 | Vermeij et al., 1980 |
| <i>P. glauca</i> (Hinds, 1844)             |    |        |      |                      |
| Kino Bay, Sonora, Mexico                   | 22 | -      | 0.69 | Vermeij et al., 1980 |
| San Felipe, Mexico                         | 33 | -      | 0.64 | Vermeij et al., 1980 |
| <i>Strioterebrum</i>                       |    |        |      |                      |
| <i>S. plumbeum</i> (Quoy & Gaimard, 1833)  |    |        |      |                      |
| Philippines Island                         | 5  | 0      | 1.80 | Present Study        |
| <i>S. swainsoni</i> (Deshayes, 1859)       |    |        |      |                      |
| Sandwich Island                            | 4  | 0      | 1.75 | Present Study        |
| <i>Terebra</i>                             |    |        |      |                      |
| <i>T. subulata</i> (Linnaeus, 1767)        |    |        |      |                      |
| Andaman                                    | 9  | 0      | 2.56 | Present Study        |
| Unknown                                    | 2  | 0      | 1.00 | Present Study        |
| Philippines Island                         | 2  | 0      | 4.50 | Present Study        |
| China                                      | 1  | 0      | 2.00 | Present Study        |
| Lubang Island(Mindoro)                     | 3  | 0      | 4.00 | Present Study        |
| Apiang, Gilbert Island                     | 13 | -      | 1.69 | Vermeij et al., 1980 |
| Larantoeika, Flores                        | 22 | -      | 1.00 | Vermeij et al., 1980 |
| Calapan, Mindoro                           | 25 | -      | 0.92 | Vermeij et al., 1980 |
| Ternay, Mahe, Seychelles                   | 16 | -      | 0.38 | Vermeij et al., 1980 |
| Motupore Island, Papua New Guinea          | 26 | -      | 0.38 | Signor, 1985         |
| <i>T. tricolor</i> G. B. Sowerby I, 1825   |    |        |      |                      |
| Andaman                                    | 10 | 0      | 3.30 | Present Study        |
| <i>T. dislocata</i> (Say, 1822)            |    |        |      |                      |
| Florida                                    | 5  | 0      | 2.00 | Present Study        |

(continues)



(continued)

| Species/Locality                          | n   | DF (%) | PF   | Reference            |
|-------------------------------------------|-----|--------|------|----------------------|
| Unknown                                   | 3   | 0      | 1.00 | Present Study        |
| Egmont Key, Florida                       | 14  | -      | 1.00 | Vermeij et al., 1980 |
| Panama City, Florida                      | 15  | -      | 0.93 | Vermeij et al., 1980 |
| Bimini, Bahamas                           | 13  | -      | 0.85 | Vermeij et al., 1980 |
| Long Boat Key, Florida                    | 20  | -      | 0.80 | Vermeij et al., 1980 |
| Anna Maria Key, Florida                   | 12  | -      | 0.75 | Vermeij et al., 1980 |
| Alicetown, Bahamas                        | 35  | -      | 0.74 | Vermeij et al., 1980 |
| Turkey Point, Florida                     | 38  | -      | 0.55 | Vermeij et al., 1980 |
| Naples, Florida                           | 39  | -      | 0.15 | Vermeij et al., 1980 |
| St. Petersburg, Florida                   | 22  | -      | 0.21 | Vermeij et al., 1980 |
| Alligator Harbor, Florida                 | 10  | -      | 0.20 | Vermeij et al., 1980 |
| Cape Lookout, North Carolina              | 22  | -      | 0.41 | Vermeij et al., 1980 |
| St. Augustine, Florida                    | 24  | -      | 0.21 | Vermeij et al., 1980 |
| Beaufort, North Carolina                  | 53  | -      | 0.13 | Vermeij et al., 1980 |
| Beaufort, North Carolina                  | 130 | 12.1   | -    | Vermeij et al., 1980 |
| Panama City, Florida                      | 15  | 0      | -    | Vermeij et al., 1980 |
| Myrtle Beach, South Carolina              | 1   | 0      | -    | Funderburk, 2010     |
| Edisto Beach, South Carolina              | 1   | 0      | -    | Funderburk, 2010     |
| Hilton Head, South Carolina               | 5   | 0      | -    | Funderburk, 2010     |
| Anna Maria Island, Florida                | 2   | 0      | -    | Funderburk, 2010     |
| <i>T. deshayesi</i> Reeve, 1860           |     |        |      |                      |
| Ceylon                                    | 3   | 0      | 2.33 | Present Study        |
| Mauritius                                 | 2   | 50     | 1.00 | Present Study        |
| Andaman                                   | 3   | 0      | 2.67 | Present Study        |
| Unknown                                   | 1   | 0      | 0    | Present Study        |
| <i>T. cumingi</i> Linnaeus, 1758          |     |        |      |                      |
| Hong Kong                                 | 1   | 0      | 1.00 | Present Study        |
| <i>T. lauretanae</i> Tenison-Woods, 1878  |     |        |      |                      |
| Port Hacking, New South Wales             | 22  | -      | 0.32 | Vermeij et al., 1980 |
| <i>T. bifrons</i> Hinds, 1844             |     |        |      |                      |
| Unknown                                   | 1   | 0      | 2.00 | Present Study        |
| <i>T. areolata</i> A. Adams & Reeve, 1850 |     |        |      |                      |
| Andaman                                   | 3   | 0      | 1.33 | Present Study        |
| <i>T. laevigata</i> (Gray, 1834)          |     |        |      |                      |
| Unknown                                   | 3   | 0      | 2.00 | Present Study        |
| Mauritius                                 | 1   | 100    | 3.00 | Present Study        |
| Andaman                                   | 1   | 0      | 3.00 | Present Study        |
| Nosy-Be, Madagascar                       | 50  | -      | 1.14 | Vermeij et al., 1980 |
| Mahe, Seychelles                          | 12  | -      | 0.67 | Vermeij et al., 1980 |
| Biak, Iran Jaya                           | 11  | -      | 0.27 | Vermeij et al., 1980 |
| Ternay Bay, Mahe                          | 39  | -      | 0.21 | Vermeij et al., 1980 |
| Motupore Island, Papua New Guinea         | 92  | -      | 0.65 | Signor, 1985         |

(continues)



(continued)

| Species/Locality                    | n   | DF (%) | PF   | Reference            |
|-------------------------------------|-----|--------|------|----------------------|
| <i>T. funiculata</i> Hinds, 1844    |     |        |      |                      |
| Unknown                             | 2   | 0      | 1.00 | Present Study        |
| Mauritius                           | 2   | 0      | 1.00 | Present Study        |
| Bay of Bengal                       | 3   | 0      | 2.00 | Present Study        |
| Honolulu, Oahu                      | 44  | -      | 0.39 | Vermeij et al., 1980 |
| Mont Lihau, Maui                    | 10  | -      | 0.20 | Vermeij et al., 1980 |
| <i>T. variegata</i> Gray, 1834      |     |        |      |                      |
| Gulf of California                  | 1   | 0      | 4.00 | Present Study        |
| California                          | 4   | 0      | 1.50 | Present Study        |
| Tres Marias Island, Mexico          | 29  | -      | 0.79 | Vermeij et al., 1980 |
| Isla Taboga, Panama                 | 101 | -      | 0.15 | Vermeij et al., 1980 |
| Puertecitos, Mexico                 | 30  | -      | 0.10 | Vermeij et al., 1980 |
| Farfan Beach, Panama                | 12  | 14     | 0.08 | Vermeij et al., 1980 |
| <i>T. longiscata</i> Deshayes, 1859 |     |        |      |                      |
| Margui Archipelago                  | 2   | 50     | 0    | Present Study        |
| <i>T. polygonia</i> Reeve, 1860     |     |        |      |                      |
| Unknown                             | 10  | 30     | 0.30 | Present Study        |
| <i>T. textilis</i> Hinds, 1844      |     |        |      |                      |
| Andaman                             | 1   | 0      | 2.00 | Present Study        |
| <i>T. glossema</i> Schwengel, 1942  |     |        |      |                      |
| Unknown                             | 1   | 0      | 1.00 | Present Study        |
| <i>T. sp.</i>                       |     |        |      |                      |
| Unknown                             | 36  | 6      | 1.22 | Present Study        |
| Madras                              | 1   | 0      | 2.00 | Present Study        |
| Sand heads                          | 22  | 27.3   | 0.46 | Present Study        |
| Vishulaka puram                     | 5   | 20     | 0.80 | Present Study        |
| Oman                                | 4   | 25     | 0.25 |                      |
| Mauritius                           | 7   | 0      | 0.57 | Present Study        |
| Venado Beach, Panama                | 12  | 66.67  | -    | Vermeij et al., 1980 |
| Nukuhiva, Marquesas                 | 21  | -      | 0.24 | Vermeij et al., 1980 |
| Longboat Key, Florida               | 2   | 0      | -    | Funderburk, 2010     |
| Honeymoon Island #1, Florida        | 6   | 0      | -    | Funderburk, 2010     |
| <i>T. babylonia</i> Lamarck, 1822   |     |        |      |                      |
| Gorokottan, Palau                   | 15  | -      | 0.69 | Vermeij et al., 1980 |
| Honolulu, Oahu                      | 13  | -      | 0.62 | Vermeij et al., 1980 |
| Aldabra Atoll                       | 12  | -      | 0.42 | Vermeij et al., 1980 |
| Tutuila, Samoa                      | 12  | -      | 0.42 | Vermeij et al., 1980 |
| Bougainville, Solomons              | 38  | -      | 0.13 | Vermeij et al., 1980 |
| <i>T. argus</i> Hinds, 1844         |     |        |      |                      |
| Honolulu, Oahu                      | 55  | -      | 0.12 | Vermeij et al., 1980 |
| <i>T. guttata</i> (Röding, 1798)    |     |        |      |                      |
| Mataeia                             | 10  | 3.00   | 0.90 | Vermeij et al., 1980 |

(continues)



(continued)

| Species/Locality                          | n  | DF (%) | PF   | Reference            |
|-------------------------------------------|----|--------|------|----------------------|
| <i>T. nodularis</i> Deshayes, 1859        |    |        |      |                      |
| Kaneohe, Oahu                             | 51 | -      | 1.26 | Vermeij et al., 1980 |
| <i>T. sp. 2</i>                           |    |        |      |                      |
| Hilo, Hawaii                              | 35 | -      | 1.43 | Vermeij et al., 1980 |
| Honolulu, Oahu                            | 81 | -      | 1.23 | Vermeij et al., 1980 |
| <i>T. pertusa</i> (Born, 1778)            |    |        |      |                      |
| Calapan, Mindoro                          | 15 | -      | 1.07 | Vermeij et al., 1980 |
| Kaanapali, Maui                           | 20 | -      | 0.70 | Vermeij et al., 1980 |
| Honolulu, Oahu                            | 52 | -      | 0.40 | Vermeij et al., 1980 |
| <i>T. concava</i> (Say, 1826)             |    |        |      |                      |
| Smith's Island, Virginia                  | 13 | -      | 0.62 | Vermeij et al., 1980 |
| <i>T. taurina</i> (Lightfoot, 1786)       |    |        |      |                      |
| Puetro Plata, Dominican Republic          | 21 | -      | 1.24 | Vermeij et al., 1980 |
| <i>T. armillata</i> Hinds, 1844           |    |        |      |                      |
| Tres Marias Island                        | 46 | -      | 0.46 | Vermeij et al., 1980 |
| <i>T. elata</i> Hinds, 1844               |    |        |      |                      |
| Gulf of Tehuantepec, Mexico               | 22 | -      | 0.55 | Vermeij et al., 1980 |
| Venado Beach, Panama                      | 21 | 21.74  | 0.38 | Vermeij et al., 1980 |
| <i>T. hancocki</i> Bratcher & Burch, 1970 |    |        |      |                      |
| Isla Taboga, Panama                       | 28 | -      | 0.43 | Vermeij et al., 1980 |
| <i>T. ornata</i> Gray, 1834               |    |        |      |                      |
| Isla Taboga, Panama                       | 14 | -      | 0.29 | Vermeij et al., 1980 |
| <i>T. plicata</i> Gray, 1834              |    |        |      |                      |
| Seymour Bay, Galapagos                    | 12 | -      | 0.83 | Vermeij et al., 1980 |
| <i>T. robusta</i> Hinds, 1844             |    |        |      |                      |
| Panama                                    | 17 | -      | 1.53 | Vermeij et al., 1980 |
| Balboa, Panama                            | 23 | -      | 1.39 | Vermeij et al., 1980 |
| <i>T. specillata</i> Hinds, 1844          |    |        |      |                      |
| Tres Marias Island                        | 13 | -      | 1.15 | Vermeij et al., 1980 |
| Santa Maria Bay, Baja California          | 22 | -      | 0.41 | Vermeij et al., 1980 |
| San Jose, Guatemala                       | 18 | -      | 0.22 | Vermeij et al., 1980 |
| <i>T. amanda</i> Hinds, 1844              |    |        |      |                      |
| Sydney, New South Wales                   | 22 | -      | 0.86 | Vermeij et al., 1980 |
| Port Jackson New South Wales              | 13 | -      | 0.74 | Vermeij et al., 1980 |
| <i>T. hemphilli</i> Vanatta, 1924         |    |        |      |                      |
| San Diego, California                     | 13 | -      | 0.31 | Vermeij et al., 1980 |
| California                                | 2  | 0      | 1.00 | Present Study        |
| <i>T. jacksoniana</i> (Garrard, 1976)     |    |        |      |                      |
| Crookhaven Heads, New South Wales         | 15 | -      | 0.13 | Vermeij et al., 1980 |
| Gerringong, New South Wales               | 15 | -      | 0.08 | Vermeij et al., 1980 |

(continues)



(continued)

| Species/Locality                      | n  | DF (%) | PF   | Reference            |
|---------------------------------------|----|--------|------|----------------------|
| <i>Triplostephanus</i>                |    |        |      |                      |
| <i>T. hoarai</i> (Drivas & Jay, 1988) |    |        |      |                      |
| Zululand                              | 1  | 0      | 2.00 | Present Study        |
| <i>T. triseriatus</i> (Gray, 1834)    |    |        |      |                      |
| Corregidor, Luzon                     | 11 | -      | 0.82 | Vermeij et al., 1980 |
| Panay                                 | 12 | -      | 0.17 | Vermeij et al., 1980 |



## POPULATION GENETIC STRUCTURE OF THE BLOOD CLAM, *TEGILLARCA GRANOSA*, ALONG THE PACIFIC COAST OF ASIA: ISOLATION BY DISTANCE IN THE SEA

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### ABSTRACT

The blood clam, *Tegillarca granosa*, is widely distributed along the coasts of the Indo-Pacific region, providing an excellent opportunity to study gene flow in sessile marine mollusks. In the present study, amplified fragment length polymorphism (AFLP) DNA markers were used to analyze the genetic structure of five blood clam populations. Genetic differentiation ( $G_{ST}$ ) and Nei's genetic distances between population pairs were found to range from 0.0245 to 0.0785 and 0.0398 to 0.1125, respectively. An AMOVA analysis showed that 89.09% of the genetic variation occurred within populations and only 10.92% occurred among populations, indicating a high degree of genetic homogeneity, probably due to considerable gene flow (average  $N_m = 7.1853$ ) among populations. Cluster analysis using the unweighted pair group method average (UPGMA) showed that geographically closer populations were clustered, suggesting isolation by distance, which was further supported by a significant positive correlation between  $G_{ST}$  and logit transformed geographic distance through a Mantel test and reduced major axis regression ( $r = 0.77$ ,  $p < 0.05$ ). The evident isolation by distance observed among blood clam populations along the Pacific coast of Asia is likely to be a consequence of both the passive larval dispersal carried by the South China Sea Warm Current and the genetic homogeneity caused by aquaculture-associated human activities.

Key words: AFLP, *Tegillarca granosa*, Isolation by distance, gene flow, Pacific coast.

### INTRODUCTION

Genetic population structure is shaped by many evolutionary factors including gene flow, genetic drift, mutation, and natural selection (Matolweni et al., 2000). Among these, gene flow, the transfer of genes or alleles between populations, is crucial to maintaining the genetic diversity of a population (McRae & Beier, 2007; Hellberg, 2009; Weersing & Toonen, 2009). Due to the inherent difficulty of direct observation, gene flow is often inferred from population genetic data and interpreted using genetic models (Rousset, 1997; Matolweni et al., 2000; Nisbikawa, 2008; Ni et al., 2011; Hirase et al., 2012). Wright's island (Wright, 1931), stepping-stone (Kimura & Weiss, 1964) and isolation by distance models (Wright, 1943) are widely used to infer gene flow among populations. Theoretically, either the

linear stepping-stone or isolation by distance can be used to model gene flow of coastal species adequately (Ni et al., 2011). Though both models predict that gene flow between populations will decrease exponentially as the geographical distance increases, the linear stepping-stone and isolation by distance apply to organisms with discrete and continuous populations, respectively (Kimura & Weiss, 1964; Casado-Amezúa et al., 2012). However, empirical studies are necessary to verify the pattern of gene flow among sessile marine bivalve populations.

The blood clam, *Tegillarca granosa* (Linnaeus, 1758), also known as the blood cockle, is widely distributed throughout the Indo-Pacific region, from the eastern coast of South Africa northwards and eastwards to Southeast Asia, Australia, Polynesia and up to northern Japan (Liu et al., 2014; Peng et al., 2015). *Tegillarca*

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*granosa*, a typical sessile bottom-dwelling bivalve, is a commercially important species, which also plays a crucial ecological role in the coastal ecosystem as an important unit in the food chain (Davenport & Wong, 1986; Shi et al., 2016). Therefore, knowledge of the population genetic structure and gene flow (connectivity) among populations of blood clam is essential for both fisheries management and the design of marine protected areas.

To our best knowledge, only a few studies have investigated the genetic structure of blood clam populations and neither the gene flow among populations nor the relationship between gene flow and geographical distance have been addressed (Li et al., 2003; Lv et al., 2005). Using 20 randomly amplified polymorphic DNA (RAPD) markers, Li (2003) showed that five relative northern *T. granosa* populations sampled from Busan (E 129°, N 35°), Rongcheng (E 122°, N 37°), Fenghua (E 121°, N 29°), Yueqing (E 121°, N 28°) and Fuding (E 120°, N 27°) were highly homogeneous along the Pacific coast of Asia. In addition, interestingly, significant genetic heterogeneity between the relative northern populations (same populations as Li studied) and southern populations sampled from Shantou (E 116.5°, N 23°) and Zhanjiang (E 110°, N 20.5°) was reported by Lv (2005) via variation analysis of 11 allozymes, suggesting a gene flow barrier between northern and southern *T. granosa* populations.

Many marine invertebrates, especially bivalves, are characterized with a prolonged planktonic larval duration (PLD), which facilitates high gene flow among geographically separated populations and mitigates the effect of genetic drift (Affinito et al., 2014). Therefore, without evident geographical barriers in the marine realm, bivalves with planktonic larvae are generally predicted to be genetically homogeneous throughout their geographical ranges, which has been widely supported by empirical studies in bivalves such as *Donax deltoides* by Murray-Jones & Ayre (1997), *Mytilus californianus* by Levinton & Suchanek (1978), *Bathymodiolus* by Miyazaki et al. (2013), *Venus antiqua* by Gallardo et al. (1998) and *Mactromeris polynyma* by Cassista & Hart (2007). Similar to many broadcasting spawning invertebrates, blood clams release gametes into the open sea. The fertilized eggs go through metamorphosis and develop into planktonic larvae feeding on microalgae and organic debris. The planktonic larval duration

(PLD) of blood clam varies from about seven days to several weeks depending on environmental factors such as temperature and salinity (You et al., 2001). Consider the long PLD and the absence of any notable geographical barrier between the northern and southern populations, the unexpected result of Lv (2005) seems to be paradoxical.

In addition, to our best knowledge, no effort has ever been made to investigate the effect of potential geographical barriers on gene flow of blood clam populations. Along the Pacific coast of Asia, a 80 km-long strait, the Qiongzhou Strait, lies between the mainland of China and Hainan Island. With the narrowest width of 18 km, it is interesting to know whether the Qiongzhou Strait will act as a barrier for gene flow of blood clam. However, previous studies exclusively investigated the blood clam populations northeastward of this strait.

In the present study, the AFLP technique was used to analyze genetic structure and gene flow of *T. granosa* populations across Qiongzhou Strait along the Pacific coast of Asia. The aims of the present work were: (1) to investigate population genetic structure, (2) to elucidate patterns of gene flow, (3) to verify whether a gene flow barrier does exist between the northern and southern populations and (4) to determine whether the Qiongzhou Strait will act as a barrier to gene flow of *T. granosa* along the Pacific coast of Asia. The results obtained in this study will not only contribute to a better understanding of *T. granosa* populations but also to our overall knowledge of gene flow in coastal marine bivalves.

## MATERIALS AND METHODS

From November 2007 to March 2008, during the low tide adult blood clams were collected from the intertidal mudflat (one spot within each sampling site) of Busan (Korea, E 129°02', N 35°06'), Yancheng (Jiangsu, China, E 120°22', N 33°05'), Yueqing (Zhejiang, China, E 120°57', N 28°07'), Haikou (Hainan, China, E 110°22', N 20°01') and Qisha (Guangxi, China, E 108°29', N 21°35') (Fig. 1) via dredge harvest method using a clam harrow. *Tegillarca granosa* populations were named after the corresponding abbreviations of sampling sites (BS, YC, YQ, HK and QS). All samples were kept alive on ice throughout shipment back to the laboratory. The adductor muscles of sampled blood clams (28 individuals for each population) were dis-



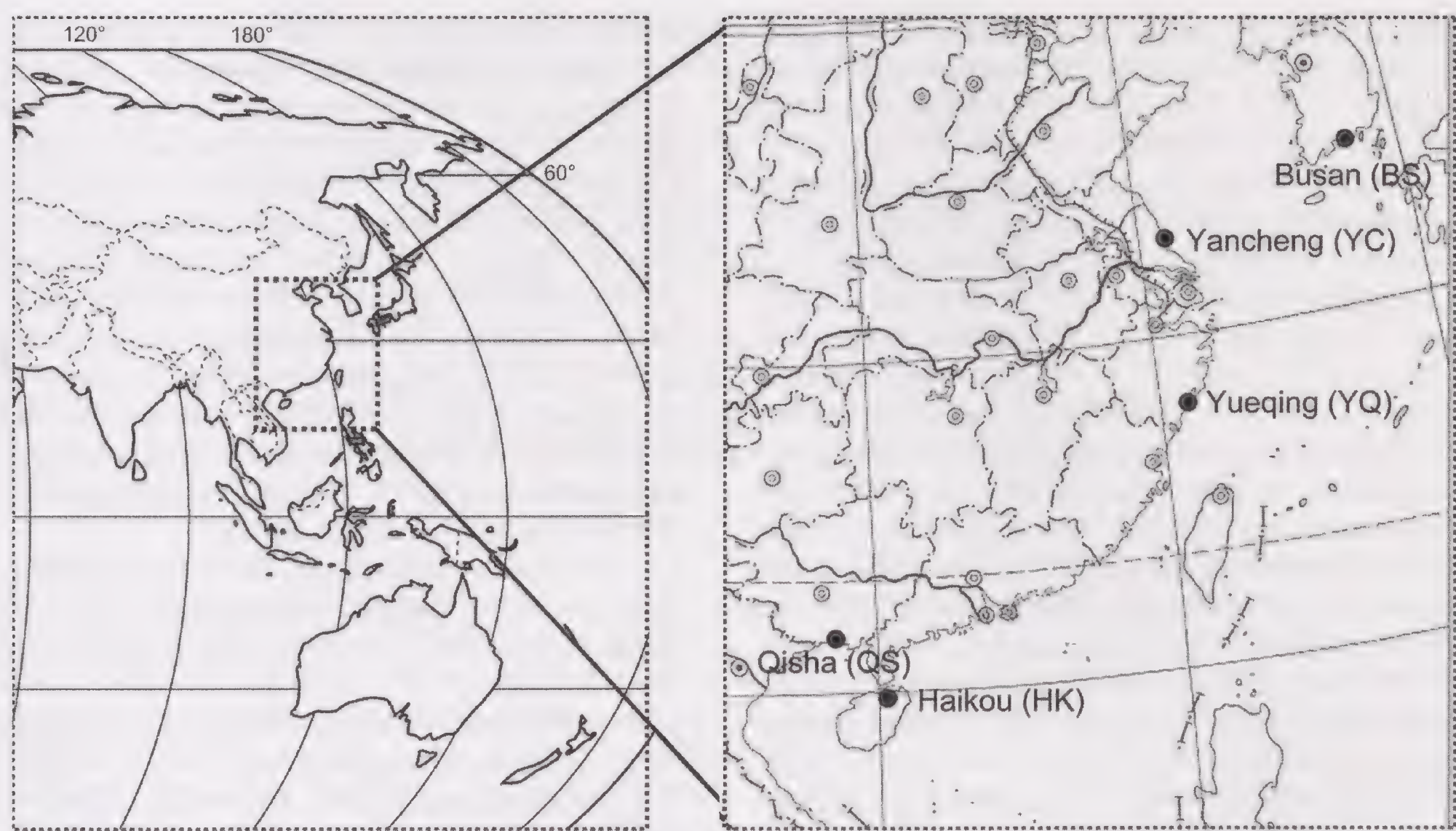


FIG. 1. Sampling sites of *T. granosa* along the Pacific coast of Asia: Busan (BS, E 129°02', N 35°06'), Yancheng (YC, E 120°22', N 33°05'), Yueqing (YQ, E 120°57', N 28°07'), Haikou (HK, E 110°22', N 20°01') and Qisha (QS, E 108°29', N 21°35').

sected and preserved separately at -80°C for further genetic analysis.

Approximately 100 mg of muscle tissue from each clam was coarsely homogenised and digested in 500 µl lysis buffer (50mmol/L Tris-HCl, ph 8.0; 1% SDS; 25 mmol/L EDTA) with 200 µg of Proteinase K (TAKARA) at 37°C overnight. The solution was then extracted twice with 25: 24: 1 phenol-chloroform-isoamyl alcohol followed by 95% ethanol precipitation at -20°C. Extracted DNA was resuspended with sterile distilled water to a final concentration 100 ng/µL.

AFLPs were generated following the protocol of Vos (Vos et al., 1995). Briefly, 100 ng genomic DNA was first digested by 2U EcoRI (TaKaRa) at 37°C for 3 h followed by 2U MseI (Fermentas life sciences) at 65°C for 20 min in a volume of 20 µL. Digested DNA was ligated with EcoRI and MseI adaptors using 1U T4 DNA ligase (TaKaRa) in a volume of 25 µL at 37°C for 3 h. A volume of 20 µL PCR reactions contained 1 µL ligated DNA, 1×PCR buffer, 1.5 mM MgCl<sub>2</sub>, 0.2 mM dNTPs, 1U Taq polymerase (TaKaRa), and 30 µM each of EcoRI and MseI primers, and were subjected to cycling conditions: 94°C

TABLE 1. Selective primer combinations used for AFLP analysis (selective primer regions in bold).

| No. | EcoRI Selective Primer              | MseI Selective Primer              |
|-----|-------------------------------------|------------------------------------|
| 1   | 5'-GACTGCGTACCAATTCA <b>AAC</b> -3' | 5'-GATGAGTCCTGAGTA <b>ACCA</b> -3' |
| 2   | 5'-GACTGCGTACCAATTCA <b>AAC</b> -3' | 5'-GATGAGTCCTGAGTA <b>ACTT</b> -3' |
| 3   | 5'-GACTGCGTACCAATTCA <b>AAG</b> -3' | 5'-GATGAGTCCTGAGTA <b>ACGA</b> -3' |
| 4   | 5'-GACTGCGTACCAATTCA <b>AGA</b> -3' | 5'-GATGAGTCCTGAGTA <b>ACTT</b> -3' |
| 5   | 5'-GACTGCGTACCAATTCA <b>ATG</b> -3' | 5'-GATGAGTCCTGAGTA <b>ACCA</b> -3' |



for two min, 30 cycles of 94°C for 30 s, 56°C for 30 s and 72°C for 60 s. The primers used were name: 5'-GACTGCGTACCAATTCA-3' and name: 5'-GATGAGTCCTGAGTAAC-3'.

The amplified products were diluted by a factor of ten and then used as templates for a second round of selective amplification. The selective amplification was performed in a 20 µL volume containing 1 µL of the diluted first round PCR product, 1 × PCR buffer, 1.5 mM MgCl<sub>2</sub>, 0.2 mM dNTPs, 1U Taq polymerase (TaKaRa) and 3.0 µM each of EcoRI and MseI selective primers. Based on the preliminary experimental results, five different selective primer combinations were used (Table 1). A gradient annealing temperature starting from 65°C with a decreasing rate of -0.7°C/cycle was used during the first 12 amplification cycles, followed by 20 cycles of amplification at the constant annealing temperature of 56°C. The denaturation and elongation conditions were similar to those used in the first round amplification. Amplified products were then separated on 6% polyacrylamide sequencing gels and visualized by silver staining.

Genotypes for each locus were scored as present '1' or absent '0' and a binary data matrix was constructed encompassing fragments in the range of 75–750 bp. To assess the genetic structure of *T. granosa* populations, the number of loci (loci with a non-zero frequency), proportions of polymorphic loci (%p), Nei's (1973) genetic diversity, and Shannon's information index (Lewontin, 1972) were estimated using POPGENE 1.31. In addition, pairwise similarities within population were calculated as  $S_{ij} = 2a/(2a + b + c)$ , where *a* is the number of bands

shared by sample *i* and sample *j*, *b* is the number of bands present only in sample *i*, and *c* is the number of bands present only in sample *j* (Nei & Li, 1979). Nei's (1972) genetic identity and genetic distance were then estimated using genetic similarity results. A dendrogram of Nei's genetic distances evaluated by the unweighed pair group method average (UP-GMA) clustering procedure was constructed by PHYLIP 3.5 (Felsenstein, 2004). Analysis of molecular variance (AMOVA) was conducted in POPGENE 1.31 to describe how variance was partitioned within and among populations (Kautenburger & Sander, 2008).

To evaluate gene flow between populations, pairwise genetic differentiations (*Gst*) were computed following the methods of Hartl & Clark (1989) and the number of migrants (*Nm*) were obtained by the formula  $Nm = (1-Gst)/4Gst$  (Slatkin & Barton, 1989). The maritime geographic distances between sampling sites were measured using the NTS-Elements D3.0 measuring tool. To avoid error that might arise from treating non-independent geographic distance as independent data in Pearson's correlation analysis, the strength and relationship between geographic distance and genetic divergence were assessed with reduced major axis regression and a Mantel test (10000 randomizations) using the program IBD 3.23 (Bohonak, 2002). The null hypothesis was supported if no relationship was observed between genetic divergences and geographic distances. This would be expected under Wright's island model, when migrants are drawn from a random pool. An alternative result supports the isolation by distance model.

TABLE 2. Loci numbers, proportions of polymorphic loci (%p), genetic similarity, Nei's gene diversity, and Shannon information index of five *T. granosa* populations.

| Popula-<br>tion | Sample<br>Size | Number<br>of loci | Proportion<br>of polymor-<br>phic loci<br>(%p) | Genetic Similarity |        |               | Nei's Gene<br>Diversity | Shannon<br>Information<br>Index |
|-----------------|----------------|-------------------|------------------------------------------------|--------------------|--------|---------------|-------------------------|---------------------------------|
|                 |                |                   |                                                | Maxium             | Minium | Mean±SD       |                         |                                 |
| BS              | 28             | 271               | 80.44                                          | 0.8125             | 0.6543 | 0.7382±0.0271 | 0.2325                  | 0.3589                          |
| YC              | 28             | 274               | 80.66                                          | 0.8138             | 0.6338 | 0.7352±0.0275 | 0.2379                  | 0.3657                          |
| YQ              | 28             | 269               | 79.93                                          | 0.8483             | 0.6690 | 0.7410±0.0267 | 0.2330                  | 0.3585                          |
| HK              | 28             | 271               | 78.97                                          | 0.8056             | 0.6755 | 0.7482±0.0266 | 0.2301                  | 0.3540                          |
| QS              | 28             | 268               | 76.87                                          | 0.8255             | 0.6849 | 0.7522±0.0263 | 0.2220                  | 0.3419                          |
| Overall         | 140            | 278               | 86.33                                          |                    |        |               | 0.2610±0.1664           | 0.4023±0.2274                   |



TABLE 3. The pairwise genetic differentiation (*Gst*, above diagonal) and genetic distances (below diagonal) of five *T. granosa* populations.

| Population | BS     | YC     | YQ     | HK     | QS     |
|------------|--------|--------|--------|--------|--------|
| BS         | -      | 0.0284 | 0.0533 | 0.0621 | 0.0775 |
| YC         | 0.0435 | -      | 0.0481 | 0.0572 | 0.0785 |
| YQ         | 0.0788 | 0.0708 | -      | 0.0326 | 0.0348 |
| HK         | 0.0910 | 0.0834 | 0.0505 | -      | 0.0245 |
| QS         | 0.1125 | 0.1123 | 0.0549 | 0.0398 | -      |

RESULTS

Population Structure and Genetic Diversity

Of a total of 278 loci identified from 140 individuals, 240 were shown to be polymorphic (86.33%) (Table 2). Overall genetic diversity and Shannon index for all individuals were 0.2610 and 0.4023, respectively, suggesting a relatively high genetic diversity for *T. granosa*. Though fairly similar among all five populations, QS and YC populations were shown to have the lowest and highest genetic diversity, respectively, which were illustrated by loci number, polymorphic loci, and genetic similarity within populations.

Genetic Differentiation

Pairwise genetic differentiation (*Gst*) was found to range from 0.0245 to 0.0785 (TABLE 3), and the overall *Gst* was  $0.0738 \pm 0.0266$ . Nei's genetic distances between populations ranged from 0.0398 to 0.1125. The biggest genetic differentiations were found between the most geographically distant populations (0.0775 between population BS and QS, and 0.0785 between population YC and QS). Similarly, the smallest genetic differentiations were found between the closest populations (0.0245 between

population QS and HK, and 0.0284 between BS and YC). This pattern was also observed in the population clustering data, in which geographically closer populations such as BS and YC were grouped together (Fig. 2). AMOVA showed that 89.09% of the genetic variation occurred within populations and only 10.92% occurred among populations (Table 4).

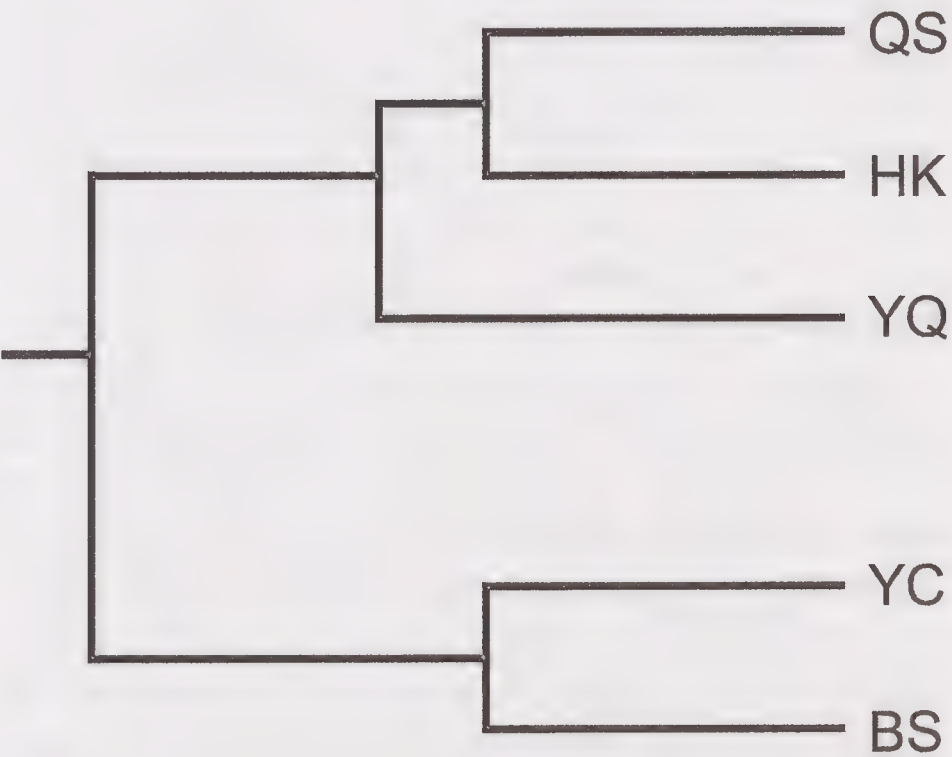


FIG. 2. Dendrogram of five *T. granosa* populations along Pacific coast of Asia based on Nei's genetic distances using the unweighed pair group method average (UPGMA) clustering procedure.

TABLE 4. Analysis of molecular variance (AMOVA) for five *T. granosa* populations.

| Source of Variance | dF  | Sum of Square | Variance Components | Percentage of Variation (%) | <i>p</i> |
|--------------------|-----|---------------|---------------------|-----------------------------|----------|
| Among populations  | 4   | 1094.34       | 6.45                | 10.92                       | < 0.001  |
| Within populations | 137 | 7208.94       | 52.62               | 89.08                       | < 0.001  |
| Total              | 141 | 8303.28       | 59.07               | -                           | -        |



TABLE 5. The maritime geographic distances (in km, above diagonal) and gene flow (Nm, below diagonal) between population pairs.

| Population | BS      | YC     | YQ      | HK      | QS      |
|------------|---------|--------|---------|---------|---------|
| BS         | -       | 921.27 | 1188.92 | 2721.32 | 2993.99 |
| YC         | 10.9875 | -      | 865.42  | 2205.61 | 2993.99 |
| YQ         | 5.8483  | 6.5604 | -       | 1390.28 | 2460.41 |
| HK         | 4.9973  | 5.4949 | 9.4009  | -       | 249.16  |
| QS         | 3.9447  | 3.9517 | 8.6053  | 12.0622 | -       |

Gene Flow

The average gene flow between pairwise populations was 7.1853, indicating a high connectivity between *T. granosa* populations (Table 5). As shown in Figure 3, there was a significant correlation between pairwise genetic differentiation and logit transformed geographic distances as demonstrated by reduced major axis regression.

DISCUSSION

Genetic diversity is critical for a population to adapt to changing environments (Reed & Frankham, 2003). In the present study, 240 out of 278 loci of 140 blood clam individuals were shown to be polymorphic. Furthermore, overall high gene diversity and Shannon index (0.2610 and 0.4023 respectively) suggest relatively high genetic diversity in *T. granosa*

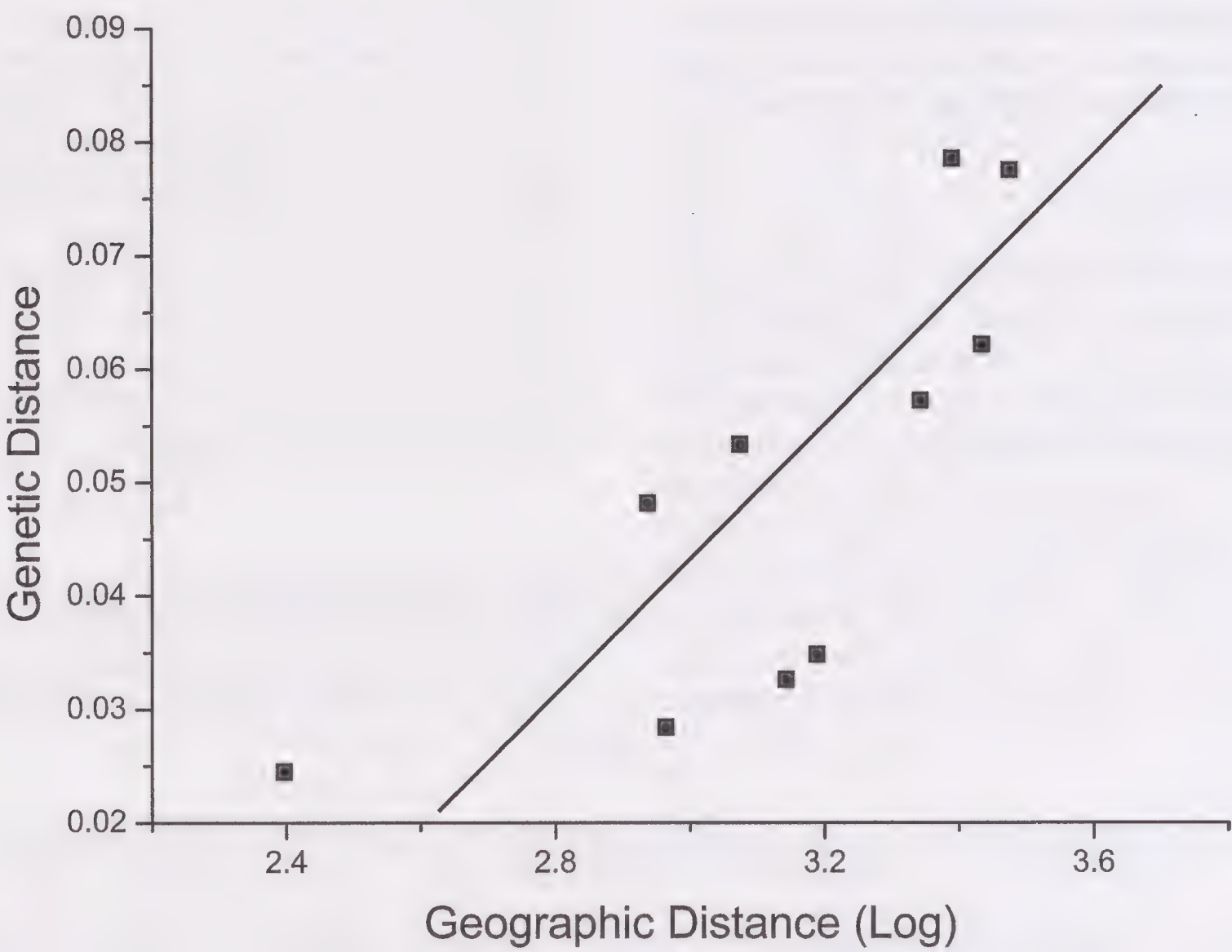


FIG. 3. Reduced major axis regression between genetic distance and logit transformed geographic distances. Genetic distance = 0.06·log (geographic distances) - 0.14 (Z = 1.60, r = 0.77, p < 0.05, Mantel test).



populations along the Pacific coast. These results are comparable to those reported in previous studies. Using the randomly amplified polymorphic DNA (RAPD) technique, Li et al. (2003) reported similar proportions of polymorphic loci ( $> 70\%$ ) and high genetic diversity of five *T. granosa* along the Pacific coast of Asia. Due to different techniques used, a much lower proportion of polymorphic loci ( $28.6\% \sim 44.4\%$ ) and high genetic diversity were revealed by allozyme variation analysis for seven *T. granosa* populations along the Pacific coast (Lv et al., 2005).

In addition, we also found that the genetic diversity of *T. granosa* populations generally increased with latitude, as high latitude populations (YC and BS) and low latitude populations (QS and HK) display the highest and lowest genetic diversities, respectively. Compared to the relatively benign environment of temperate areas, *T. granosa* living in southern tropical areas such as Qisha (QS) and HaiKou (HK) experience a more fluctuating environment. For instance, typhoons occur almost every year during the spawning season of blood clam in these southern locations, which lead to dramatic fluctuations in salinity, temperature, water movement, and food availability (Luo et al., 2014). Considering the fact that planktonic larvae of blood clam are sensitive to environmental factors such as temperature and food availability (You et al., 2001), the environmental fluctuations may therefore reduce the recruitment and lead to poor persistence of genetic diversity.

High genetic homogeneity was revealed in this study based on the low levels of genetic differentiation ( $G_{ST}$ ) and Nei's genetic distances among *T. granosa* populations investigated. This conclusion was further supported by the AMOVA analysis which showed only 10.92% of the genetic variation occurred among *T. granosa* populations. Comparative results have been reported in several other bivalve species (Murray-Jones & Ayre, 1997; Levinton & Suchanek, 1978; Miyazaki et al., 2013). For instance, using allozyme analysis, Murray-Jones & Ayre (1997) found 12 *Donax deltoides* populations separated up to 1,200 km along the east Australian coast were highly homogeneous. Similar results were reported in *Mytilus californianus* over 1,000 km (Levinton & Suchanek, 1978) and *Bathymodiolus* up to 1,500 km (Miyazaki et al., 2013) as well.

Fundamentally, population structure is highly determined by the interaction between gene flow and genetic drift (Hutchison & Templeton, 1999). Therefore, the results of the present study indicate that a significant degree of gene flow occurs among geographically distant *T. granosa* populations (average pairwise distance, 1,654 km) along the Pacific coast of Asia without notable barriers to gene flow between northern and southern populations or between populations separated by the Qiongzhou Strait. The wide distribution along the tropical, subtropical, and temperate Pacific coast of Asia and the extensive gene flow (average  $N_m = 7.1853$ ) among studied populations are probably due to high degree of dispersal.

Many benthic marine invertebrates, especially bivalves, are broadcast spawners possessing pelagic gametes and larvae (Crean & Marshall, 2008; Schmidt-Roach et al., 2012). However, gene flow through active swimming of sperm is highly restricted in marine bivalves due to the limited locomotory ability (Liu et al., 2011). Furthermore, gene flow through dispersal of sperm is unlikely since sperm of *T. granosa* will lose their fertilization ability shortly after spawning due to the effect of dilution and a relatively short half-life (Levitan et al., 1991; Levitan & Petersen, 1995). The passive movement of pelagic eggs and larvae advected by currents could partially explain the long distance dispersal of *T. granosa*. In this circumstance, gene flow through dispersal is largely influenced by both the ecological characteristics and environmental factors such as hydrodynamics. The prolonged planktonic larval period of *T. granosa* (seven days to several weeks depending on environmental factors of the seawater) provide adequate time for long-distance passive dispersal. Moreover, the strong pressure-driven South China Sea Warm Current (SCSWC) from the southern coast of China northeastwards during the spawning season of *T. granosa* probably acts as the carrier for larval dispersal (Hsueh & Zhong, 2004). This pattern is similar to that seen in the sea star, *Acanthaster planci*, along the Ryukyus and the coast of Asia (Nishida & Lucas, 1988), so the high genetic homogeneity of *T. granosa* may be a result of significant gene flow through water current as well.

Even with a strong current, the maximal travel distance of entrained larvae within this current is about several hundred kilometers (Marko, 2004), which is significantly shorter than most



of the geographical distances between the paired *T. granosa* populations investigated. Moreover, the existence of geographic and/or ecological barriers between populations and the complexity of hydrodynamics along the edge of continents may disrupt larval dispersal as well (Borrero-Pérez et al., 2011; Lessios, 2012; Sá-Pinto et al., 2012).

In order to interpret the strong gene flow across such a vast geographical distance, the effect of the occasional events and human activities should be considered as well. Previous studies suggest that invertebrates may achieve long distance dispersal by occasional events such as rafting via attachment to small floating debris (Hellberg, 2009; Nakajima et al., 2010). Since blood clam spawns several times during the spawning season and produces approximate  $10^6$  eggs for one spawning of a female (Wang & Wang, 2008), large fecundity may make the impact of occasional dispersal events prominent. Whether intentional or not, human activities may facilitate the dispersal of marine invertebrates such as the bivalve, *Musculista senhousia*, over long geographical distances (Asif & Krug, 2012). As an important aquaculture species, mature adult blood clams were often shipped over relatively short distances along the coast from a few kilometers up to hundred kilometers for the purpose of breeding (Wang & Wang, 2008). In turn, the blood clam seeds produced by the breeding industries were sold to surrounding coastal areas. Both the shipment of adult and juveniles will lead to a constant gene flow among adjacent populations. Therefore, the isolation by distance model detected in present study probably was accomplished through both larvae dispersal and human activities.

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## COLD SNAILS IN HOT SPRINGS: OBSERVATIONS FROM PATAGONIA AND THE TIBETAN PLATEAU

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### ABSTRACT

Patagonia and the Tibetan Plateau both harbor various freshwaters with relatively low temperatures. Pulmonate freshwater gastropods are widely distributed in these water bodies. Both regions, however, also possess a number of geothermal hot springs. Such springs might have served as refugia for freshwater taxa during the Pleistocene. In the present study, two hot spring systems, one in Patagonia and one at the Tibetan Plateau, were examined. Individuals of *Chilina patagonica* (in Patagonia) as well as *Radix* cf. *auricularia* and *Gyraulus* sp. (at the Tibetan Plateau) were found living in the warm water. These taxa typically live at much lower water temperatures. At the Patagonian hot spring system, gastropods occurred continuously from warm to cold water. Analyses of mitochondrial DNA sequence data revealed very close relationships of Tibetan Plateau hot spring gastropods to cold water populations. Acclimatization and not adaptation is thus probably the main thermal adjustment process involved. Given these findings, it is plausible that hot springs have served as glacial refugia for these freshwater gastropods.

Key words: *Chilina patagonica*, *Radix* cf. *auricularia*, *Gyraulus* sp., geothermal hot springs, glacial refugia, thermal acclimatization.

### INTRODUCTION

With distributions ranging almost worldwide, freshwater gastropods occupy a wide range of temperature niches (van der Schalie & Berry, 1973). Some taxa are stenothermic, for example, the tropical species *Melanoides tuberculata* Müller, 1774, which requires warm water (Mitchell & Brandt, 2005), or European spring snails (*Bythinella* spp.), which arguably depend on low water temperatures (Radoman, 1976; but see Benke et al., 2011). Others, however, such as the invasive species *Pomacea canaliculata* (Lamarck, 1819) and *Potamopyrgus antipodarum* (Gray, 1843), tolerate much wider temperature ranges and are able to live in various climatic regions (Mochida, 1991; Wada & Matsukura, 2007; Alonso & Castro-Díez, 2008).

In general, the highest diversity of freshwater gastropods exists in the tropics, decreasing at higher latitudes (Strong et al., 2008). However, some freshwater gastropod species

have been successful in very cool regions. Prime examples are found in Patagonia and at the Tibetan Plateau. Patagonia is a region in southern South America, which includes the southern parts of Chile and Argentina. While eastern Patagonia is characterized by a cold and dry climate with steppe vegetation, western Patagonia is relatively cold and wet and mostly covered by forest and moorland (McEwan et al., 1997). The Tibetan Plateau, which is located in Central Asia, has an average elevation of about 5,000 m above sea level (a.s.l.) and is characterized by a cold climate with alpine meadow, steppe and desert vegetation (Herzschuh et al., 2006). Patagonia and the Tibetan Plateau harbor various freshwater systems with relatively low water temperatures (Schmid-Araya, 1993; Walker & Yang, 1999; Soto et al., 2007). Freshwater gastropod taxa belonging to the pulmonate (Hygrophila) genera *Chilina* (in Patagonia) as well as *Radix* and *Gyraulus* (at the Tibetan Plateau), however, are widespread and abundant in these regions and inhabit vari-

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ous freshwater habitats, such as rivers, lakes and ponds (Rumi et al., 2006; Oheimb et al., 2011, 2013).

Beside these cold water systems, both Patagonia and the Tibetan Plateau possess a number of geothermal hot springs, discharging hot groundwater and creating pools with high water temperatures (Lahsen, 1988; Kearey & Wei, 1993; Hamza & Muñoz, 1996; Hochstein & Regenauer-Lieb, 1998; for a definition of hot springs: Pentecost et al., 2003). In central-southern Chile, for instance, about 30 hot spring areas are known, and at least half of them exceed temperatures of 60°C (Lahsen, 1988). At the Tibetan Plateau along the Xizang-Yunnan geothermal zone, for example, over 400 hot water environments, including hot springs, have been detected, with some of them reaching boiling point (summarized in Kearey & Wei, 1993). Many of the hot springs, however, are uninhabitable for multicellular organisms because of their adverse chemical composition or temperatures being too high (Kearey & Wei, 1993; Hofmann, 2012; Clarke, 2014). In any event, temperatures of these springs contrast sharply with those of surrounding cold water systems.

In Patagonia as well as at the Tibetan Plateau, repeated glacial periods during the Pleistocene epoch resulted in enormous climatic fluctuations (Rabassa & Clapperton, 1990; Lehmkuhl & Owen, 2005). For instance, during the Last Glacial Maximum (approx. 20,000 ago) large parts of Patagonia were covered by a massive ice sheet (Hulton et al., 2002), and the Tibetan Plateau underwent huge glaciations and increased aridification (Lehmkuhl, 1998; Lehmkuhl & Owen, 2005). The role of hot springs as glacial refugia for freshwater organisms during these times is subject to ongoing debate (e.g., Fraser et al., 2014; Pointing et al., 2014).

Given this background, the present study aims to examine freshwater gastropods in Patagonian and Tibetan Plateau hot springs and to evaluate relationships of hot spring and cold water snails.

## MATERIAL AND METHODS

During field trips to Patagonia and the Tibetan Plateau the freshwater gastropod fauna in two geothermal hot spring systems was studied.

The survey in Patagonia took place in December 2009. The examined two springs were part of the “Termas de Porcelana” at the Comau Fiord, Los Lagos Region, Chile

(-42.457940°, -72.456023°; 89 m a.s.l.). Both springs were connected to a stream with colder water (12.1°C). The spring located further downstream (Fig. 1) formed a small basin with a gradual transition from warm (40.5°C) to cold (12.5°C). Nearby and further upstream another warm water spring (up to 33.1°C) flowed directly into the cold stream, causing a sharp transition in temperature. In both springs, the flow velocity of the water was relatively low and thick layers of algal biofilm were apparent, while in the cold stream amounts of algae were much lower. Measurements of temperature and specific conductivity were taken with a Hanna Combo pH & EC hand instrument.

Observations at the Tibetan Plateau were carried out in October 2011. The sampling site was a spring complex located in Chutsen (Wenquan) at the northeastern Tibetan Plateau, Qinghai Province, China (35.4050°, 99.4299°; 3,938 m a.s.l.; Fig. 2; see also Weynell et al. 2016). The spring complex had approximate dimensions of 100 m by 30 m. It included several separate hot springs that partially flowed into pools with water temperatures > 45°C. These pools were used for laundry by local people. Considerable amounts of waste were present among the springs. Lush algae grew throughout much of the spring complex. Temperature, specific conductivity, and pH were measured using a portable Hach HQ40d instrument. Elevations for both examined hot spring systems were inferred using the SRTM (Shuttle Radar Topography Mission) dataset.

Hot spring gastropod specimens were either preserved initially in 95% and later in 70% ethanol (Patagonian specimens) or constantly in 80% ethanol (Tibetan Plateau specimens). Patagonian voucher material has been deposited at the Natural History Museum of Vienna, Tibetan Plateau voucher material at the Systematics and Biodiversity Collection of the University of Gießen (UGSB). Eleven Tibetan Plateau specimens were used for genetic analyses (Table 1). DNA was isolated from foot tissue of individual gastropods using the protocol of Winnepenninckx et al. (1993). A 655 base pair fragment of the cytochrome *c* oxidase subunit I (COI) gene was amplified using the primers LCO1490 (Folmer et al., 1994) and COR722b (Wilke & Davis, 2000; this primer is a slight modification of the Folmer et al. (1994) primer HCO2198). DNA sequencing (forward and reverse) was conducted on an ABI 3730 XL sequencer (Life Technologies) using the Big Dye Terminator Kit (Life Technologies). All sequences have been deposited at GenBank (accession numbers KT326304–KT326314;



Table 1). Sequence data were either trimmed to 600 bp and combined with the 600 bp *Radix* COI dataset from Oheimb et al. (2011) or combined with the 655 bp *Gyraulus* COI dataset from Oheimb et al. (2013). For alignment, Clustal W (Thompson et al., 1994) implemented in BioEdit 7.2.5 (Hall, 1999) was used. Parsimony network analyses were carried out using TCS 1.21 (Clement et al., 2000).

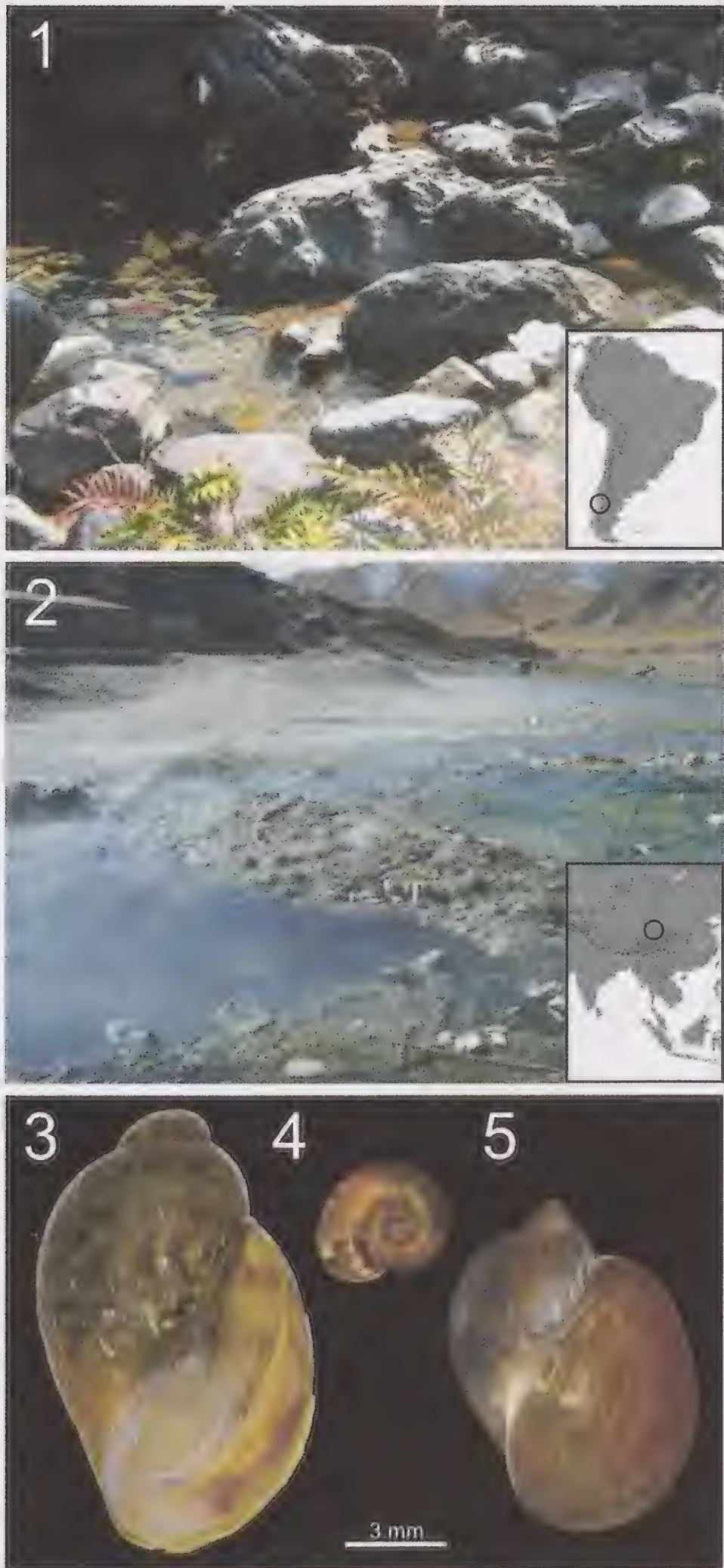
## RESULTS

At the Patagonian hot spring system, individuals of the genus *Chilina* were found at both studied springs (Fig. 3). Specimens occurred in water temperatures up to 34.5°C (conductivity of 1005  $\mu\text{S cm}^{-1}$ ) at the downstream spring and up to 33.1°C (720  $\mu\text{S cm}^{-1}$ ) at the upstream spring. No gastropods were found at higher temperatures. Eggs could be detected at both; copulating individuals only at the upstream spring. *Chilina* individuals were observed grazing on biofilms. At the downstream spring with its gradual transition from warm to cold water, *Chilina* individuals were found along the entire temperature gradient (up to 34.5°C). In both springs, specimens occurred in high densities and showed a strong spatial clustering. Densities decreased with decreasing water temperatures. The adjacent cold stream was sparsely inhabited by individuals of the genus *Chilina*, morphologically indistinguishable from the individuals found at higher temperatures, as well as by gastropods of the family Cochliopidae. No cochliopid specimens were found near the warmer areas.

The *Chilina* specimens from the springs and the adjacent cold stream were determined as *Chilina patagonica* G. B. Sowerby II, 1874, based on shell morphology and coloration (including a comparison to the type specimens stored at the Natural History Museum London), and on their geographic distribution (G. B. Sowerby II, 1874; Smith, 1881; Castellanos & Gaillard, 1981).

At the Tibetan Plateau hot spring complex (pH 7.92), individuals of the genera *Radix* and *Gyraulus* were found (Figs. 4, 5). High densities of *Radix* specimens occurred at a water temperature of 29.2°C (conductivity of 1194  $\mu\text{S cm}^{-1}$ ). Furthermore, a few scattered *Radix* and *Gyraulus* individuals were present at a second location within the spring complex that had a water temperature of 40.3°C (conductivity of 1513  $\mu\text{S cm}^{-1}$ ). No gastropods were found in the pools with water temperatures > 45°C. No other mollusk taxa were present in the hot spring complex.

Three different COI haplotypes were found among the six sequenced hot spring *Radix* specimens. A parsimony network analysis, including the COI dataset from Oheimb et al. (2011), revealed that the hot spring haplotypes differ from a haplotype of *Radix* cf. *auricularia* found in cold water habitats at the Tibetan Plateau (belonging to Clade 1; Oheimb et al., 2011) by one to two mutational steps (Fig. 6). Tibetan Plateau *R.* cf. *auricularia* are very closely

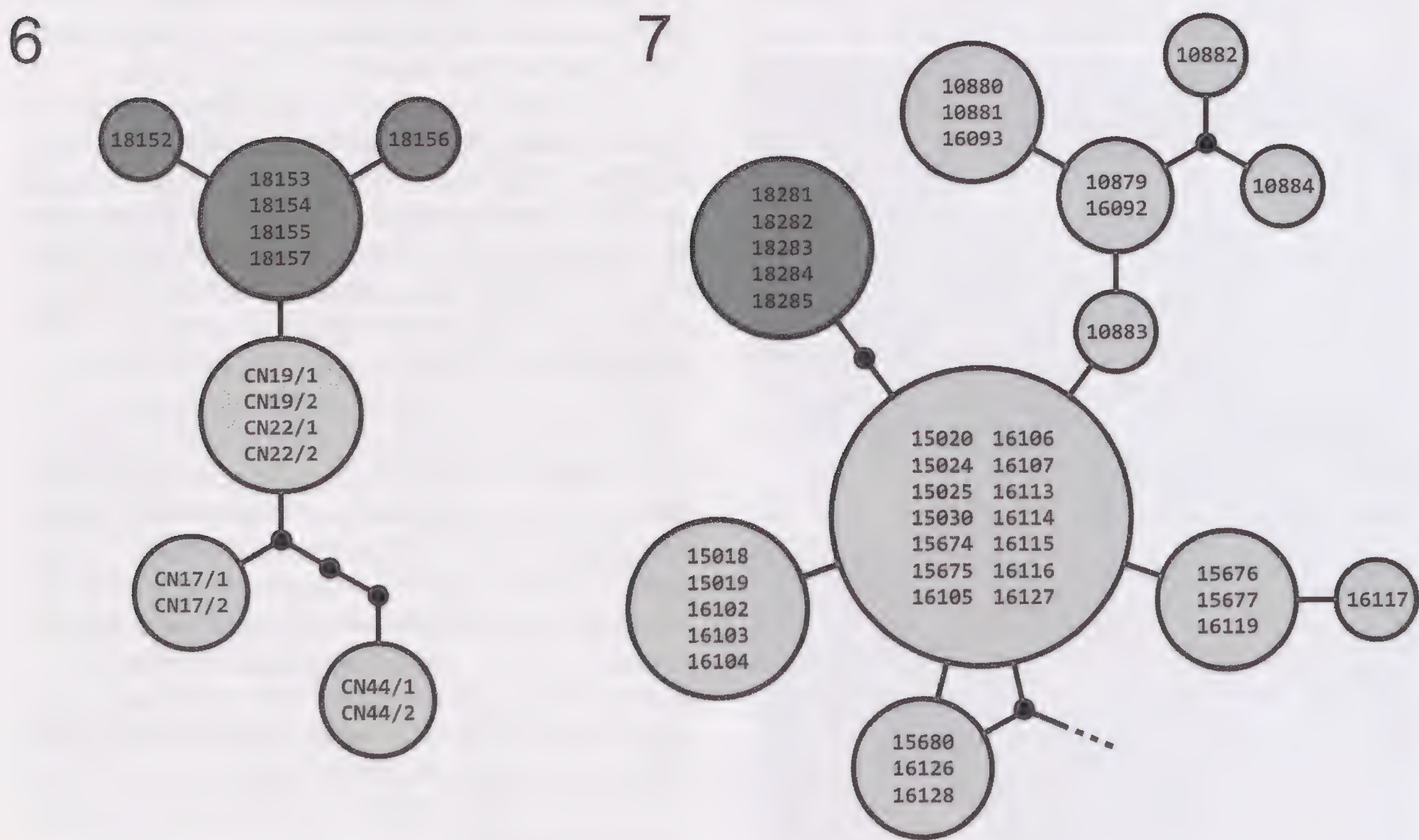


FIGS. 1–5. Studied hot spring systems in Patagonia (FIG. 1) and at the Tibetan Plateau (FIG. 2), and representative specimens of hot spring *Chilina patagonica* (FIG. 3), *Gyraulus* sp. (FIG. 4; UGSB 10372), and *Radix* cf. *auricularia* (FIG. 5; UGSB 10150).



TABLE 1. List of genetically studied gastropod specimens from the Tibetan Plateau, including taxon, voucher details and GenBank accession numbers. The voucher material has been deposited at the Systematics and Biodiversity Collection of the University of Giessen (UGSB).

| Taxon                               | DNA voucher no. | Specimen voucher no. | GenBank accession no. |
|-------------------------------------|-----------------|----------------------|-----------------------|
| <i>Radix</i> cf. <i>auricularia</i> | 18152           | UGSB 10146           | KT326304              |
| <i>Radix</i> cf. <i>auricularia</i> | 18153           | UGSB 10147           | KT326305              |
| <i>Radix</i> cf. <i>auricularia</i> | 18154           | UGSB 10148           | KT326306              |
| <i>Radix</i> cf. <i>auricularia</i> | 18155           | UGSB 10149           | KT326307              |
| <i>Radix</i> cf. <i>auricularia</i> | 18156           | UGSB 10150           | KT326308              |
| <i>Radix</i> cf. <i>auricularia</i> | 18157           | UGSB 10151           | KT326309              |
| <i>Gyraulus</i> sp.                 | 18281           | UGSB 10368           | KT326310              |
| <i>Gyraulus</i> sp.                 | 18282           | UGSB 10369           | KT326311              |
| <i>Gyraulus</i> sp.                 | 18283           | UGSB 10370           | KT326312              |
| <i>Gyraulus</i> sp.                 | 18284           | UGSB 10371           | KT326313              |
| <i>Gyraulus</i> sp.                 | 18285           | UGSB 10372           | KT326314              |



FIGS. 6, 7. Statistical parsimony networks of *Radix* (FIG. 6) and *Gyraulus* (FIG. 7) based on the mitochondrial COI gene. The networks include Tibetan Plateau hot spring specimens (dark gray) and cold water specimens (light gray) from the datasets of Oheimb et al. (2011) (*Radix*) and Oheimb et al. (2013) (*Gyraulus*). Only sub-networks including hot spring specimens are shown (applying a 95% connection limit). The *Gyraulus* network comprises the whole clade N2 from Oheimb et al. (2013) and is shown only in parts. Labels refer to DNA voucher numbers (see Table 1) and to specimen codes from the literature.



related to other lineages of the widespread species *Radix auricularia* (Linnaeus, 1758) (Oheimb et al., 2011). Given these findings, all studied Tibetan Plateau hot spring specimens are considered as *Radix* cf. *auricularia* (Clade 1 *sensu* Oheimb et al., 2011).

All five sequenced *Gyraulus* specimens shared the same COI haplotype. A parsimony network, including the Oheimb et al. (2013) COI dataset, revealed that the hot spring haplotype is separated by two mutational steps from a Tibetan Plateau haplotype (belonging to Clade N2; Oheimb et al., 2013) present in cold water habitats (Fig. 7). Given the lack of adequate taxonomic studies on Tibetan Plateau *Gyraulus* spp. (see also Oheimb et al., 2013), all studied hot spring specimens are considered as *Gyraulus* sp. (Clade N2 *sensu* Oheimb et al., 2013).

## DISCUSSION

Inhabiting geothermal hot springs in cool climates can bring various advantages for freshwater snails. In comparison to the surrounding cold water bodies, hot springs exhibit little seasonal variation in average temperature (as shown by Mackenzie et al. (2013) for the “Termas de Porcelana”). Higher levels of dissolved ions in the water (particularly of calcium carbonate; Brues, 1924) can be beneficial for the growth of gastropod shells. The hot spring systems examined in this study (in Patagonia and at the Tibetan Plateau) were characterized by large amounts of algae compared to nearby colder water bodies. Herbivorous snail species might benefit from this, probably year-round, food supply. Moreover, it can be assumed that snail taxa living in these hot springs face little interspecific competition from other freshwater organisms. At the Patagonian hot spring system, for example, other freshwater gastropods, which were observed in surrounding water bodies, were not present in the thermal springs. Likewise, predation may be less important in hot springs. However, hot springs might also entail problems for freshwater snails. Warmer water holds less oxygen and sometimes hot springs can contain poisonous chemicals (Brues, 1924). In addition, high temperatures alone can harm organisms (Clarke, 2014). Some springs exhibit occasional temperature fluctuations that can reach or exceed maximum thermal tolerance limits of gastropods (e.g., Mladenka & Minshall, 2001).

A number of gastropods that are restricted to hot springs have been reported (e.g., Myler & Minshall, 2000; Mladenka & Minshall, 2001; Hershler et al., 2011; Sîrbu et al., 2013). However, all three gastropod taxa that have been found living in hot springs in this study, typically inhabit relatively cold water bodies in Patagonia and at the Tibetan Plateau (Castellanos & Gailard, 1981; Oheimb et al., 2011, 2013; Landler & Oheimb, 2013; P. V. v. Oheimb & L. Landler, personal observation). Thus, they might originally have colonized the hot springs from surrounding cold water habitats. Two general processes can allow individuals or populations to gain adjustments to changed thermal conditions: acclimatization and adaptation. While during acclimatization individuals adjust by phenotypic (particularly physiological) plasticity over comparatively short time scales, during adaptation natural selection drives changes within populations over comparatively longer time scales (Lagerspetz, 2006; Hofmann & Todgham, 2010). Thus, a thermal acclimatization is usually a reversible adjustment (Lagerspetz, 2006). A thermal adaptation involves functionally relevant changes to the genome and therefore leads to a stronger dependence of organisms to their specific environment.

The fact that *Chilina patagonica* specimens occurred continuously from warm spring water to cold stream water, including the transition zone in between, indicates that individuals are able to switch between different temperature conditions. Therefore, thermal acclimatization of individual gastropods is probably the major process involved. Also Tibetan Plateau hot spring *Radix* cf. *auricularia* and *Gyraulus* sp. may have acclimatized to their habitat as analyses of DNA sequence data revealed that both are very closely related to cold water populations. As *R. auricularia* is a very widely distributed species, which inhabits various regions outside the Tibetan Plateau (Glöer, 2002; Oheimb et al., 2011), this taxon may generally have a high potential for thermal acclimatization. Although acclimatization might thus be the main thermal adjustment process in the studied hot spring taxa, adaptation cannot be excluded. Experimental and physiological studies should be carried out for explicitly testing the hypothesis of thermal acclimatization.

Geothermal areas might have served as refugia during the Pleistocene for various taxa (Pointing et al., 2014), especially for freshwater organisms. Pérez-Losada et al. (2011), for example, assumed hot springs as glacial refugia



for freshwater crustaceans (*Aegla alacalufi* Jara & López, 1981) within the area of the Patagonian ice sheet, and Hofmann (2012) supposed hot spring refugia for hot spring snakes (*Thermophis baileyi* (Wall, 1907)) at the southern-central Tibetan Plateau. Oheimb et al. (2011) argued that extant Tibetan Plateau *Radix* taxa have survived the Last Glacial Maximum at the plateau. Given that *C. patagonica* as well as Tibetan Plateau *R. cf. auricularia* and *Gyraulus* sp. live in hot springs today, and that they may have the ability to acclimate to such temperature regimes, it is plausible that such systems have served as glacial refugia for them. Future studies using phylogeographical approaches (see, e.g., Provan & Bennett, 2008) should thus focus on testing whether specific geothermal areas have formed glacial refugia for these gastropods.

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## SPECIES OF *LOTHIA* (GASTROPODA: LEPETIDAE) FROM SHALLOW WATERS OF THE MAGELLAN REGION

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### ABSTRACT

The Lepetidae are currently assumed to be represented by only one valid species in the Magellan region: *lothia emarginuloides* (Philippi, 1868), of which *Tectura* (*Pilidium*) *coppingeri* Smith, 1881, and *lothia coppingeri magellanica* Linse, 2002, were regarded as synonyms. The extant records of this species are scarce, although they suggest a wide distributional range in the Pacific Ocean, from off Concepción (36°S) to the Beagle Channel (55°S), and a restricted distribution in the Atlantic Ocean, where the species is only known from the Malvinas / Falkland Islands and Isla de los Estados (about 54.5°S). This study provides new information on the occurrence of the genus *lothia* in the Magellan region, including morphological, anatomical and molecular evidence. The synonymy of *Tectura* (*Pilidium*) *coppingeri*, *lothia coppingeri magellanica* and *lothia emarginuloides* is ratified. The species is properly redescribed and figured, and its intraspecific variability discussed, particularly regarding its relation with depths. Furthermore, the distribution of this species in the southwestern Atlantic is extended north to San Matías Gulf (about 41°S). *lothia megalodon* Warén, Nakano & Sellanes, 2011, previously known from deep waters off Concepción (36°S), is here reported for the first time for the Magellan region. Its finding in shallow waters from the Beagle Channel greatly extends its distribution both latitudinally and bathymetrically.

Key words: South America, Patellogastropoda, limpet, diversity.

### INTRODUCTION

The Lepetidae Gray, 1850, comprises a poorly-known family of patelliform limpets that live subtidally, usually attached to hard-substrata of deep or cold waters (Dantart & Luque, 1994; Warén et al., 2011). *lothia* Forbes, 1849, is the only member of this family thus far known from the shallow waters of southern South America. Most records of *lothia* from this area were historically assigned to *lothia coppingeri* (Smith, 1881), even when this species was regarded as a [possible] synonym of the previously described *I. emarginuloides* (Philippi, 1868) (e.g., Strebel, 1907; Hain, 1990). The alternative usage of these names seems to have originated in the combination of several facts: the unreliability of the original description of *lothia emarginuloides*, which is rather poor and lacking of details and figures; the absence of a subsequent redescription; the loss of the type material of this species; and the little understanding of the species variability, due

to the few documented records of *lothia* in the Magellan region (e.g., Cárdenas et al., 2008; Linse, 2002; Reid & Osorio, 2000; Strebel, 1907; Warén et al., 2011). Despite these uncertainties, Warén et al. (2011), based on the fact that these two taxa “were described from nearby localities (separated by maximum 400 km at the same latitude)” accepted the synonymy of these two taxa, and consequently used the older available name, *I. emarginuloides*, to refer to the species. Within the synonymy of this species, Warén et al. (2011) also included *lothia coppingeri magellanica* Linse, 2002, a subspecies originally described based on radular differences of specimens from south of Tierra del Fuego in contrast to the illustrations of an Antarctic specimen provided by Hain (1990). As a consequence, only one *lothia* species appears at present recognized as valid from the shallow waters of the Magellan region.

Warén et al. (2011) provided excellent photographs of the shell and radula of specimens they identified as *lothia emarginuloides* from

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off Concepción and Golfo de Ancud, Chile. However, the authors did not redescribe the species. Because of this, it is hard to interpret the two shell sculpture morphologies reported by the authors (i.e., the “almost smooth” shallow-water specimens from the Magellan Strait, and the “invariably sculptured” shells of deep-water specimens from southern Chile and Antarctica) as extremes of variation of a single species.

Another species, *lothia megalodon* Warén, Nakano & Sellanes, 2011, has been described from southern South America. However, this species is thus far only known from the deep-waters (methane seep) off Concepción, Chile.

Given the paucity of records of members of *lothia* in shallow waters of the Magellan region, the aims of this contribution are: (1) to provide new information on the occurrence of this genus in the area; (2) to properly redescribe and figure the intraspecific variability of *I. emarginuloides*, particularly regarding its relation with depths; and (3) to consider such intraspecific variability in the distinction of this species with *I. megalodon*.

## MATERIALS AND METHODS

The main source of information for this study comes from 42 benthic samples, obtained in the shallow waters of the Magellan region (i.e., south of 40°S on both Atlantic and Pacific coasts). Sampled sites are: San Matías Gulf (Río Negro Province), Puerto Deseado (Santa Cruz Province), Beagle Channel (Tierra del Fuego Province) and Comau Fjord (southern Chile). The samples from the San Matías Gulf were collected by diving with a 2 mm mesh-size hand-net, while those coming from the other sampled areas were obtained with a trawl operated from a ship. Living specimens of *lothia* were sorted from the sediment under stereoscopic microscope and fixed in 5% sea-water formalin (for morphological and anatomical studies) or 96% ethanol (for molecular studies).

The above-mentioned material is deposited at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Buenos Aires; the Museo de La Plata (MLP), La Plata; and the Museo de Zoología de la Universidad de Concepción (MZUC), Concepción. Number of specimens (sp.) or empty shells (s.) in each studied lot is indicated in the material exam-

ined sections. For comparative purposes the type material of *Tectura (Pilidium) coppingeri*, housed at The Natural History Museum (NHMUK), London and the type material of *lothia coppingeri magellanica*, housed at the Zoologisches Museum der Universität Hamburg (ZMH), Hamburg, were examined. Other complementary material from the studied area was examined at the ZMH, MACN, the Zoologisches Museum Berlin (ZMB), Berlin and the Museo Nacional de Historia Natural (MNHNCL), Santiago. The provided synonymies only refer to the original descriptions and to those records within the Magellan region, for which the identity of the material reported can be confirmed.

Shell measurements were taken with a micrometric eyepiece mounted in a stereoscopic microscope. They comprise length (L): maximum antero-posterior distance; width (W): maximum left-right distance perpendicular to L; height (H): maximum dorso-ventral distance; apex position (AP): length from anterior margin to apex; anterior (AW) and posterior width (PW): width perpendicular to L at the anterior and posterior fourths of the shell. The ratios W/L, H/L, AP/L, and AW/PW are provided, including the standard deviation (SD) and number of specimens considered (n). Shell morphology was figured with an AxioCam MRc Zeiss® Camera and Scanning Electron Microscope (SEM).

Radulae and jaws were dissected under stereoscopic microscope, cleaned with a 5% sodium hypochlorite solution, and mounted for SEM. For the description of the jaw (“oral cuticle”, according to Mikkelsen (1996)), the nomenclature used by Vortsepneva et al. (2013) was followed.

For molecular studies, a slice of foot tissue was sectioned, and DNA extracted with a CTAB protocol. PCR was conducted following Nakano & Ozawa (2007), using primers designed by D. J. Eernisse (pers. comm.). PCR products were sent out to Macrogen Inc. (Korea) for sequencing in both ways. Contigs were built in DNA Baser Sequence Assembler v4 (www.DnaBaser.com), and resulting sequences aligned by using ClustalW in Mega 6 (Tamura et al., 2013). A Neighbor Joining tree was built in MEGA 6, using K2P model (following Warén et al., 2011). TIM3+G model was selected as the best evolutionary model using AIC criterion in jModelTest 0.1.1 for Bayesian analysis performed in MrBayes (Huelsenbeck & Ronquist, 2001). Newly obtained sequences have been



uploaded to GenBank; voucher specimens information and accession numbers are provided in the Material examined sections. For comparative purposes the sequences of *Iothia emarginuloides*, *I. megalodon*, *I. fulva* (Müller, 1776) and *Bathylepeta linsae* Schwabe, 2006, previously obtained by Warén et al. (2011), were used, the latter as outgroup.

## SYSTEMATICS

Family Lepetidae Gray, 1850  
Genus *Iothia* Forbes, 1849

*Iothia emarginuloides*  
(Philippi, 1868)

(Figs. 1–3, 5–7, 9–11, 13, 14,  
16–20, 22, 24, 25, 27, 28)

*Patella* (?) *emarginuloides* Philippi, 1868: 224.  
*Tectura (Pilidium) coppingeri* Smith, 1881: 35,  
pl. 4, fig. 12, 12a.

*Lepeta coppingeri* E. A. Smith – Pilsbry, 1891:  
71, pl. 39, figs. 20, 21.

*Lepeta emarginuloides* Philippi – Pilsbry,  
1891: 71.

*Pilidium coppingeri* E. A. Smith – Strebel, 1907:  
110, pl. 3, fig. 38a, b.

*Lepeta (Pilidium) coppingeri* (Edg. Smith) –  
Thiele, 1912: 185.

*Lepeta coppingeri* (E. A. Smith) 1881 – Car-  
celles, 1950: 52, pl. 1, fig. 16; Carcelles, 1953:  
164, pl. 1, fig. 12.

*Iothia coppingeri magellanica* Linse, 2002: 62  
(but not figs. 9.1.1 1–4, as mentioned by the  
author).

*Iothia coppingeri* (Smith, 1881) – Reid & Oso-  
rio, 2000: 119, fig. 7A.

*Iothia coppingeri* Smith, 1881 – Cárdenas et  
al., 2008: 207, fig. 2.11.

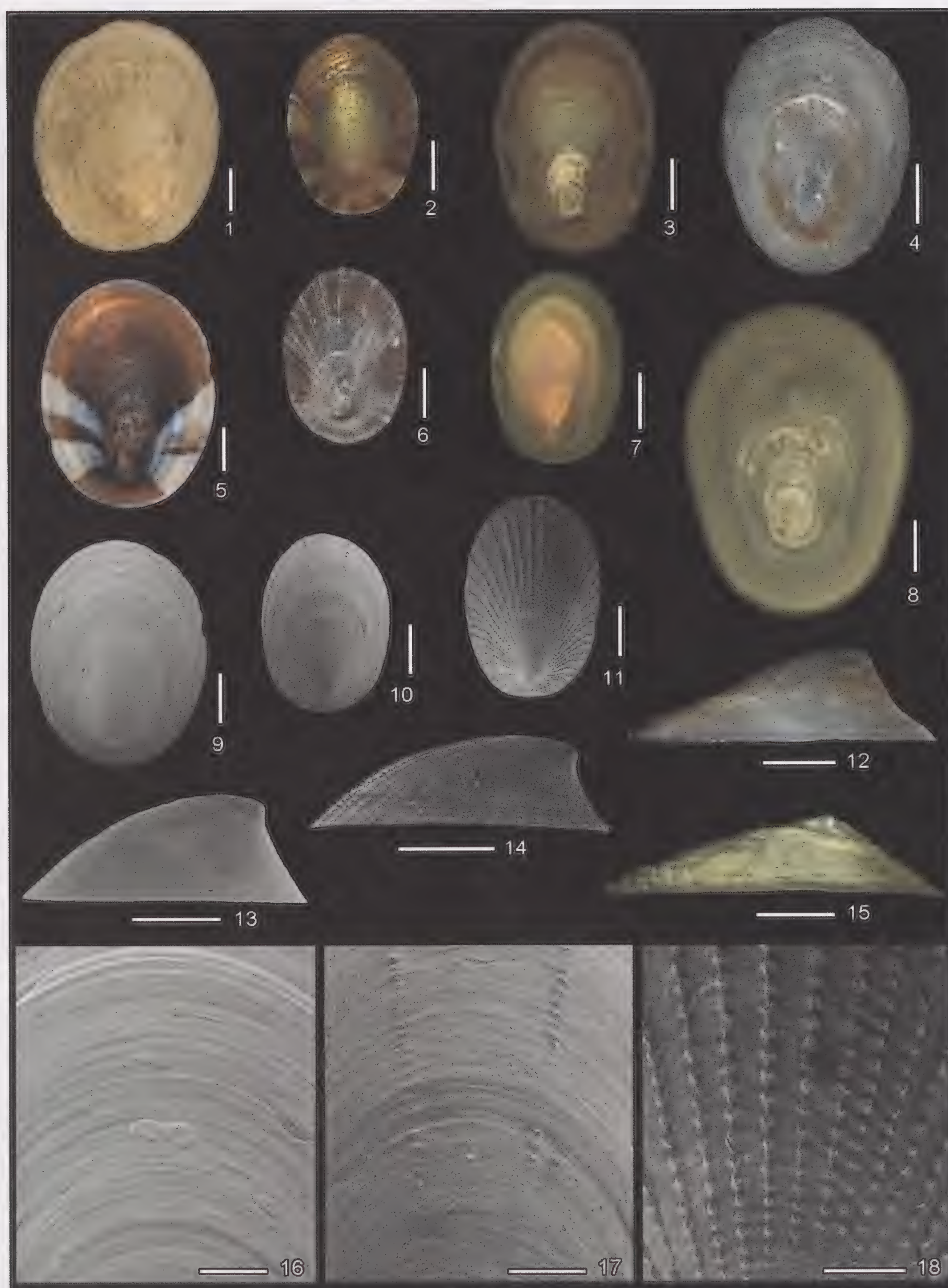
*Iothia emarginuloides* (Philippi, 1868) – Warén  
et al., 2011: 4, figs. 5, 6, 16–18, 23–26.

*Type localities*: “Magallanes” (*Patella* (?)  
*emarginuloides*). H.M.S. *Alert*, station 7,  
[53°10'S 70°56'W], Sandy Point [= Punta Arenas],  
Magellan Strait, 9–10 fms. [16–18 m] (*Tectura*  
(*Pilidium*) *coppingeri*). 55°07'18"S  
66°52'47"W, Punta Rico, 25 m (*Iothia cop-*  
*pingeri magellanica*).

*Material examined*: Holotype of *Tectura (Pi-*  
*lidium) coppingeri* (NHMUK 1879.10.15.41);  
3 paratypes of *Iothia coppingeri magellanica*  
(ZMH 2851). Golfo San Matías: Orenco:

40°50'57"S 64°36'25"W, 18 m (MACN-In  
40211: 1 sp.; DNA voucher, KU057970).  
Las Grutas: 40°50'12.8"S 65°04'42.2"W,  
10 m (MACN-In 40212: 9 s.); 40°53'32.7"S  
65°06'32.2"W, 12 m (MACN-In 40213: 1  
s.); 40°56'27.2"S 65°07'58.2"W, 10–11 m  
(MACN-In 40214: 3 s.). Playas Doradas:  
41°38'06.6"S 65°00'55.9"W, 10 m (MACN-In  
40215: 1 s.); 41°39'03.1"S 65°00'38.3"W, 12–  
14 m (MACN-In 40216: 9 s.); 41°39'41.3"S  
65°00'32.9"W, 16 m (MACN-In 40217:  
10 s.); 41°40'17.8"S 65°00'27.8"W, 16 m  
(MACN-In 40218: 2 sp., 79 s.). Puerto Lo-  
bos: 41°58'03.9"S 65°03'27.6"W, 15–18 m  
(MACN-In 40219: 1 sp., 3 s.; DNA voucher,  
KU057969); 41°58'22.8"S 65°03'28.6"W,  
16.5 m (MACN-In 40220: 3 sp., 40 s.);  
41°59'16.6"S 65°03'32.7"W, 15 m (MACN-  
In 40221: 1 sp.; DNA voucher, KU057968);  
42°00'07.0"S 65°03'20.8"W, 21 m (MACN-In  
40222: 9 s.); 42°00'54.2"S 65°03'40.9"W,  
10–12 m (MACN-In 40223: 68 s.). Puerto  
Deseado: 47°45'21.5"S 65°52'12.2"W  
(MACN-In 40224: 2 sp.); 47°45'25.2"S  
65°52'35.7"W (MACN-In 40225: 2 sp., 9  
s.); 47°45'40.4"S 65°51'00.5"W, (MACN-In  
40226: 11 sp.); 47°45'39.2"S 65°51'06.5"W  
(MACN-In 40227: 9 sp.); 47°45'41.5"S  
65°50'59.2"W (MACN-In 40228: 2 sp.);  
47°45'46.3"S 65°50'56.6"W (MACN-In  
40229: 13 sp.); 47°45'49.3"S 65°50'19.6"W  
(MACN-In 40230: 6 sp.). Magellan Strait:  
52°17'54.5"S 68°21'48.2"W, Punta Dun-  
geness (MACN-In 40231: 1 s.); [53°10'S  
70°56'W], Punta Arenas (MACN-In 12378: 6  
sp., 2 s.; ZMB unnumbered: 1 sp.; [53°30'S  
69°30'W], Bahía Inútil, 50–70 m (MACN-In  
37799: 3 s.); [53°58'S 70°35'W], Isla Dawson,  
Puerto Harris (MACN-In 12420: 1 sp.). Bea-  
gle Channel: Bahía Achicoria: 54°51'09.2"S  
68°32'38.9"W, 17–18 m (MACN-In 40232:  
1 sp.; DNA voucher, KU057971). Bahía  
Lapataia: 54°52'S 68°32'W, 27–29 m (MLP-  
Ma 14154: 8 sp.); 54°51'S 68°19'W, 5–10 m  
(MLP-Ma 14155: 7 sp.); 54°52'S 68°30'W,  
32–33 m (MLP-Ma 14156: 3 sp.). Punta Oc-  
cidental: 54°49'S 68°16'W, 24–32 m (MLP-  
Ma 14157: 4 sp.); 54°50'S 68°15'W, 18–21 m  
(MLP-Ma 14158: 66 sp.); 54°50'S 68°14'W,  
21 m (MLP-Ma 14159: 1 sp.); 54°49'S  
68°14'W, 11 m (MLP-Ma 14160: 2 sp., 1 s.);  
54°52'S 68°13'W, 12–20 m (MLP-Ma 14161:  
8 sp., 2 s.); 54°51'S 68°09'W, 22 m (MLP-  
Ma 14162: 1 sp.); 54°51'S 68°02'W, 27 m  
(MLP-Ma 14163: 37 sp., 1 s.). Islas Bridges:  
54°50'00.6"S 68°15'63.0"W, 30 m (MACN-In





FIGS. 1–18. Shell morphology. FIGS. 1–11: Dorsal view; FIGS. 12–15: Lateral view; FIGS. 16–18: Detail of posterior shell sculpture. FIGS. 1–3, 5–7, 9–11, 13, 14, 16–18. *lothia emarginuloides*. FIG. 1: *Tectura (Pilidium) coppingeri*, holotype (NHMUK 1879.10.15.41); FIGS. 2, 5, 9, 13, 16: Specimens from Puerto Lobos, 10–12 m (MACN-In 40223); FIG. 3: Specimen from Comau Fjord, 10–70 m (MZUC); FIG. 6: Specimen from Cabo San Pío, 30–35 m (MLP-Ma 14169); FIG. 7: Specimen from Isla Gable, 15–20 m (MLP-Ma 14166); FIGS. 10, 17: Specimen from Punta Occidental, 18–21 m (MLP-Ma 14158); FIGS. 11, 14, 18: Specimens from Punta Occidental, 27 m (MLP-Ma 14163). FIGS. 4, 8, 12, 15. *lothia megalodon*. FIGS. 4, 12: Specimen from Bahía Achicoria, 17–18 m (DNA voucher, KU057972); FIGS. 8, 15: Specimens from Comau Fjord, 10–70 m (MZUC). Scale bars: Figs. 1–15 = 1 mm, Figs. 16–18 = 300  $\mu$ m.



40233: 1 sp.). Remolinos: 54°52'S 67°52'W, 25 m (MLP-Ma 14164: 5 sp., 2 s.). Isla Gable: 54°53'S 67°42'W, 66–68 m (MLP-Ma 14165: 5 sp., 9 s.); 54°54'S 67°21'W, 15–20 m (MLP-Ma 14166: 20 sp., 3 s.). Isla Becasses: 54°57'S 67°01'W, 30–40 m (MLP-Ma 14167: 260 sp., 73 s.). Punta Moat: 55°01'S 66°42'W, 15–20 m (MLP-Ma 14168: 28 sp., 59 s.). Cabo San Pío: 55°03'S 66°37'W, 30–35 m (MLP-Ma 14169: 27 sp., 22 s.); 55°06'S 66°29'W, 65–80 m (MLP-Ma 14170: 18 sp., 8 s.). Southern Chile: Comau Fjord: 42°14'23"S 72°31'09"W, 10–70 m (MZUC: 26 s.); 42°22'50"S 72°25'57"W, 50–97 m (MZUC: 8 sp.); 42°24'26"S 72°25'25"W, 26–144 m (MZUC: 2 s.); 45°24'69"S 72°51'64"W, 200 m (MNHCL 7163: 1 sp.).

**Distribution:** Southeastern Pacific Ocean, from Concepción, Chile (36°22'S) (Warén et al., 2011) to Cape Horn (56°S) (Linse, 2002); through the Magellan Strait and Beagle Channel (Warén et al., 2011; this study), to Malvinas / Falkland Islands (Strebel, 1908); and extending northwards, in the southwestern Atlantic, to San Matías Gulf (40°50'S), Argentina (this study). Living specimens: 5 to 843 m. Concerning the occurrence of the species in sub-Antarctic and Antarctic waters, see discussion.

**Habitat:** Living specimens were found on hard substrates: rocks, shell fragments, polychaete tubes or living bivalves (such as the mytilid *Aulacomya atra* (Molina, 1782)).

**Redescription:** Shell small (maximum L observed = 5.8 mm), limpet-shaped, relatively high ( $H/L = 0.44 \pm 0.04$ ,  $n = 20$ ), equilateral, delicate to moderately solid (Figs. 1–3, 5–7, 9–11, 13, 14). Base ovate-elongate to regularly ovate ( $W/L = 0.73 \pm 0.05$ ,  $n = 20$ ); maximum W at about 54% of length from anterior margin; anterior end about as wide as posterior one ( $AW/PW = 0.98 \pm 0.02$ ,  $n = 10$ ). Anterior and posterior margins evenly curved; right and left margins widely arcuate to almost straight (Figs. 1–3, 5–7, 9–11, 13, 14). Apex small, somewhat inflated, anteriorly recurved, located at anterior fourth ( $AP/L = 0.18 \pm 0.05$ ,  $n = 10$ ), not extending beyond shell base; pointed in well preserved specimens (although usually eroded in larger ones). Protoconch absent in all studied specimens (minimum L observed = 1.7 mm). Anterior slope straight to slightly concave; posterior slope markedly convex, thrice the

length of the anterior one (Figs. 13, 14).

Shell surface translucent to opaque; evenly white, yellowish or brownish, or with yellowish and brown stains or radial bands (Figs. 2, 3, 5–7). Sculpture widely variable (Figs. 9–11, 13, 14, 16–18): from almost “smooth” (with only growth marks) to having well-marked radial ribs, sometimes with nodulose or scaly elements, evenly distributed all along shell surface or restricted to anterior and posterior slopes; sometimes with weak radial ribs, thinner than commarginal sculpture.

Inner shell surface smooth, similar in appearance to outer shell surface, evidencing outer color pattern, and mimicking the sculpture. Radula with about 40 rows of teeth, each with a median tooth, flanked by four teeth on each side (Figs. 19, 20). Median tooth with large, ovate base, and smooth, arrow-shaped (sharply pointed) cusp (Figs. 19, 22, 24). First two (“lateral”) teeth on each side of median tooth with solid, elongate base, gradually widening towards the cusp, which is smooth, roundly curved at the cutting edge (Figs. 22, 24). Outermost pairs of teeth (“uncini”) delicate, similar in size, with long, narrow shaft and feather-like cusps, the latter having smooth inner and deeply serrate outer margins (Figs. 19, 20, 24, 25). Teeth similar in size along the rows.

Jaw large, arcuate, smooth; anterior band markedly thickened, evenly curved, with deeply concave frontal edge (Figs. 27, 28).

#### Intraspecific Variability of *lothia emarginuloides*

According to the present study, *lothia emarginuloides* shows great variability in shell morphology, color and sculpture. Shells vary from delicate to moderately solid; translucent to variably colored; having elongate to regularly ovate base; with or without radial ribs, which, when present, may be regularly distributed over the surface or restricted to some particular areas, and may be strongly or weakly nodulose. The material here studied suggests that variation in shell shape is frequently related to the size of the specimens: smaller specimens are usually elongated, with the lateral margins of the base almost straight, whereas larger specimens are regularly ovate, with the lateral margins of the base regularly arcuate. Concerning the color of the shell, specimens from the shallow-waters from the northern part of the distribution (at both Atlantic and Pacific sides) are mostly strongly colored, whereas most of the specimens from Tierra del Fuego tend to be translucent. With





FIGS. 19–29. Radulae and jaws. FIGS. 19–21: Anterior portion of radula; FIGS. 22, 23: Detail of teeth, slightly tilt backwards; FIG. 24: Lateral view; FIGS. 25, 26: Detail of outermost (uncinal) teeth cusps; FIGS. 27–29: Jaw (arrowheads pointing frontal edge of anterior band). FIGS. 19, 20, 22, 24, 25, 27, 28. *Iothia emarginuloides*. FIG. 19: Specimen from Islas Bridges, 30 m (MACN-In 40233); FIGS. 20, 24: Specimen from Puerto Lobos, 16.5 m (MACN-In 40220); FIGS. 22, 28: Specimen from Puerto Lobos, 15 m (DNA voucher, KU057968); FIGS. 25: Specimen from Punta Occidental, 18–21 m (MLP-Ma 14158); FIG. 27: Specimen from Cabo San Pío, 65–80 m (MLP-Ma 14170). FIGS. 21, 23, 26, 29. *Iothia megalodon*. Specimen from Bahía Achicoria, 17–18 m (DNA voucher, KU057972). Scale bars: Fig. 19 = 50 µm; Figs. 20–25 = 20 µm; Fig. 26 = 10 µm; Fig. 27 = 200 µm; Figs. 28, 29 = 100 µm.



reference to shell surface, Warén et al. (2011: 6) related the sculpture with depth. According to the authors “specimens from shallow water in the Magellan Strait often have an almost smooth shell”, whereas “large Antarctic and deep water specimens [from 700–800 m depth] ... are invariably sculptured”. However, this conclusion is not in agreement with our findings, which show that weakly (“smooth”) and strongly sculptured specimens are found co-existing in the shallow waters; and this variability is not related to the size. We did not succeed either in relating such variability to the substrate where the animals live (such as reported by Nakano & Spencer (2007) for *Notoacmea scapha* (Suter, 1907)).

Taking into account that all the above-mentioned shell variants can be found at a single site and that no radular differences were found among specimens with different shell morphologies, it is here accepted that all of them correspond to a single species. Under this assumption, the three *lothia* taxa described from Magellan region (namely, *I. emarginuloides*, *I. coppingeri* and *I. coppingeri magellanica*) may be regarded as variants of a single species, being *I. emarginuloides* the oldest available name to refer to the entity.

*lothia megalodon* Warén,  
Nakano & Sellanes, 2011  
(Figs. 4, 8, 12, 15, 21, 23, 26, 29)

*lothia megalodon* Warén, Nakano & Sellanes,  
2011: 6, figs. 7, 8, 10–14, 19–22.

*Type locality*: 36°22.01'S 73°43.10'W, off Concepción, Chile; 764–843 m.

*Material examined*: Beagle Channel: Bahía Achicoria: 54°51'09.2"S 68°32'38.9"W, 17–18 m (MACN-In: 40234: 1 sp.; DNA voucher, KU057972). Isla Gable: 54°53'S 67°42'W, 66–68 m (MLP-Ma 14171: 1 sp., 1 s.). Southern Chile: Comau Fjord: 42°14'23"S 72°31'09"W, 10–70 m (MZUC: 5 s.).

*Distribution*: Southeastern Pacific Ocean, from Concepción (36°22'S) (Warén et al., 2011), Chile, to Beagle Channel (54°53'S) (this study); living from 17 to 843 m; empty shells found up to 10 m depth.

*Remarks*: The species was properly described in its original description, thus a redescription herein is considered unnecessary.

## MOLECULAR RESULTS

The Neighbour Joining and Bayesian inference trees were congruent, showing monophyletic reciprocity for both *lothia emarginuloides* and *I. megalodon* (Fig. 30). Bootstrap and posterior probability values were maximum for these species (100/100). P-distances obtained showed within group values of 0.0028 for *lothia emarginuloides* and 0.0258 for *I. megalodon*. The genetic distance between both species was 0.188.

## DISCUSSION

The present study provides morphological, radular and molecular evidence that confirms the presence of two species of *lothia* in the Magellan region: *I. emarginuloides* and *I. megalodon*. This finding reveals that the assertion by Warén et al. (2011), that *I. emarginuloides* and *I. coppingeri* belong to a single species, cannot longer be based on the proximity of their type localities. Moreover, the statement that their “type specimens are very similar” cannot be actually confirmed, because the type material of *I. emarginuloides* is apparently lost; at least, it was not found in the collections of the MNHNCL nor at the ZMB, where other species described from Chile by Philippi are housed (nor in other museum collections; E. V. Coan pers. comm., Oct. 2015). Consequently,

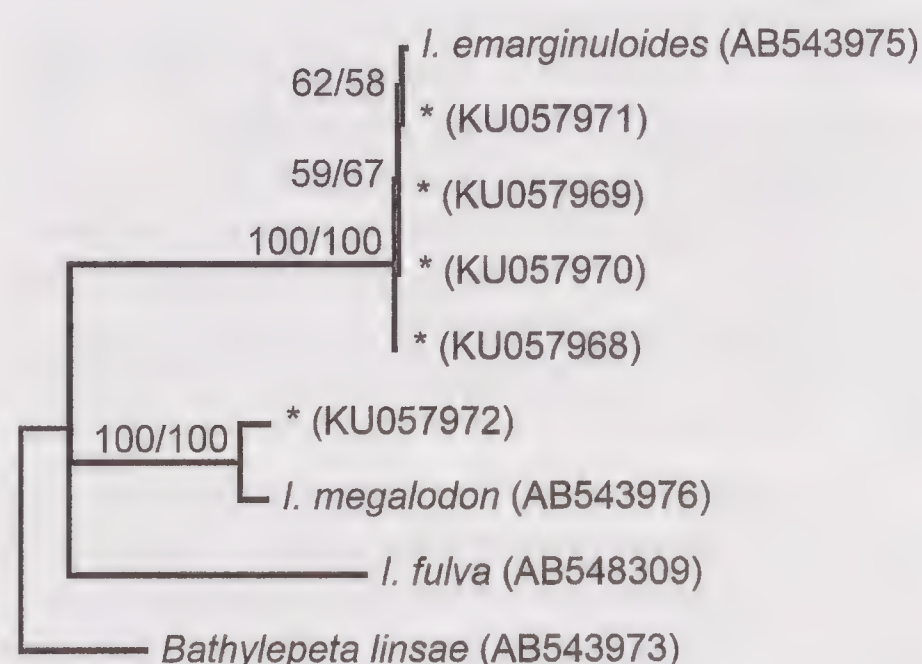


FIG. 30. Neighbor Joining and Bayesian trees strict consensus. Numbers above nodes show bootstrap values and Bayesian posterior probabilities (values below 50 are not shown). Terminal names correspond to identifications from GenBank and accession numbers; \*= newly sequenced material (detailed in material examined sections).



the best alternative to solve this issue is to understand well the intraspecific variability of the taxa occurring in the Magellan Region, and consider such variability in the context of the original descriptions.

*Lothia megalodon* can be clearly distinguished from *L. emarginuloides* by its pear-shaped base of shell, with the anterior end much narrower than the posterior one ( $AW/PW = 0.89 \pm 0.01$ ,  $n = 5$ ), by being more markedly depressed ( $H/L = 0.27 \pm 0.03$ ,  $n = 4$ ), and by having a less overhanging apex which, in addition, is somewhat more posteriorly located ( $AP/L = 0.28 \pm 0.03$ ,  $n = 5$ ) (Figs. 4, 8, 12, 15 vs. 1–3, 5–7, 9–11, 13, 14). Moreover, the posterior slope is almost straight in *L. megalodon*, whereas it is widely convex in *L. emarginuloides*. Warén et al. (2011) reported as additional distinctive characters for *Lothia megalodon* the presence of abnormally large radular teeth, with one bicuspid lateral tooth on each side of the median tooth, and the two pairs of outermost teeth (“uncini”) having an almost smooth edge at the “apical part”. The larger size of the anterior teeth and the bicuspid nature of the innermost lateral teeth were confirmed herein (Figs. 21, 23). However, regarding the outermost lateral teeth, both the radulae of *L. megalodon* showed by Warén et al. (2011: fig. 24), and that coming from the specimen studied herein (Figs. 23, 26), actually have the outer margin of the cutting edge serrated (instead of “almost smooth”). Despite this contradiction, the cutting edge still remains as a useful character for distinguishing the two species: *L. megalodon* has a rounded distal tip, and relatively few, serrations at the outer margin, whereas *L. emarginuloides* has sharply pointed distal tip, and a greater number of deeper serrations.

The study of the jaws revealed another previously disregarded difference between these two species: in *L. emarginuloides* the frontal edge of the anterior band is centrally concave, whereas in *L. megalodon* it is convex (Figs. 27, 28 vs. 29).

*Lothia emarginuloides* was originally described as having an ovate outline, scaly ribs and eyes at the base of the cephalic tentacles. These characters allow to differentiate the species from *L. megalodon*, which has a pear-shaped outline, “low spines, knobs or blisters”, and the animal lacks eyes.

Given that it is clearly distinguishable from any other *Lothia* species, we find no reason for designating a neotype for *Lothia emarginuloides* (following ICZN, 1999: Article 75). The species has been properly redescribed (herein) and figured (in Warén et al., 2011; and herein).

## Geographic and Bathymetric Distribution of the Species

Previous documented records of *Lothia emarginuloides* in the Magellan region come from southern Chile (Cárdenas et al., 2008; Reid & Osorio, 2000; Strebel, 1907; Warén et al., 2011), the Magellan Strait (Ageitos de Castellanos & Landoni, 1988; Linse, 2002; Smith, 1881; Strebel, 1907), the Beagle Channel (Linse, 2002; Linse & Brandt, 1998; Strebel, 1907; Warén et al., 2011), south of Tierra del Fuego (Linse, 2002), Cape Horn (Rochebrune & Mabilie, 1889), Isla de los Estados (Castellanos, 1980; Dell, 1990) and Malvinas / Falkland Islands (Strebel, 1908; Powell, 1951; Ageitos de Castellanos & Landoni, 1988).

The material examined as part of this study provides new information on the occurrence of this species in almost all these areas, at the time that considerably extends the previously known distributional range of the species in the southwestern Atlantic, north to Golfo San Matías ( $40^{\circ}50'12.8''S$ ). The finding of *Lothia emarginuloides* in the shallow waters of the Golfo San Matías has two intrinsic connotations: (1) it allows to confirm the presence of the genus in shallow waters of intermediate latitudes, contrary to that previously stated by Warén et al. (2011), who reported that “shallow water species occur only in high latitudes”; and (2) has significance for the study of the biogeographic limits between the Magellan and Argentine Provinces. According to the previous literature, it has been traditionally assumed that such limit is located in Península Valdes (at about  $42\text{--}43^{\circ}S$ ) (e.g., Balech & Ehrlich, 2008; Boschi, 2000). The present study reveals that, *Lothia emarginuloides* is one of the species that surpass the  $42^{\circ}S$  “limit”, and extends northwards, entering the San Matías Gulf (although, according to the currently available information, not extending beyond this gulf).

Concerning the occurrence of *Lothia emarginuloides* in Chile, it should be considered that the northernmost (shallow-depth) records of the species come from Valdivia (Dell, 1990). Warén et al. (2011) also reported the species from off Concepción ( $36^{\circ}S$ ), central Chile, at 764–843 m depth, an area also under the influence of Magellanic waters, that at  $35\text{--}45^{\circ}S$  deflect from the coast, and continue northwards by deep waters (Thiel et al., 2007).

“*Lothia coppingeri*” was reported from several sub-Antarctic and Antarctic sites as well (e.g., Arnaud, 1972; Canteras & Arnaud, 1985; Dell, 1990; Eales, 1923; Hain, 1990; Hedley, 1916;



Powell, 1951, 1958; Troncoso et al., 2001), from where *Lothia antarctica* (Smith, 1907) and *Lothia fulviformes* (Egorova, 1972) were also described. The conspecificity of this material with *Lothia emarginuloides* deserves further studies.

*Lothia megalodon* was previously regarded as a methane seep species, based on the fact that until now it was only known from its original description, at deep waters off Concepción (central Chile). The new finding here provided considerably extends its known distribution both latitudinally (southwards up to the Beagle Channel) and bathymetrically (extending to shallow waters), also revealing that it is not a species restricted to the methane seeps.

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## RESEARCH NOTES







*BURNUPIA INGAE* LANZER, 1991 (GASTROPODA: HYGROPHILA):  
CONTRIBUTIONS TO THE KNOWLEDGE ON ITS MORPHOLOGY AND  
FIRST RECORDS IN RIO DE JANEIRO STATE, BRAZIL

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INTRODUCTION

*Burnupia* Walker, 1912, is a genus of freshwater limpet traditionally considered as belonging to the Ancyliidae (Pilsbry & Bequaert, 1927; Hubendick, 1964; Brown, 1994; Lanzer, 1996; Hodgson & Healy, 1998), or included in the tribe Ancylini in the superfamily Planorboidea (Bouchet & Rocroi, 2005). However, its taxonomic position is controversial: based on similarity of radula morphology Pilsbry (1920) suggested a close relationship between *Burnupia* and South American *Uncancylus* Pilsbry, 1913. Brown (1965) placed this genus into the family Ferrissiidae, whereas Burch (1962) proposed a close relationship between *Burnupia* and *Laevapex* forming the subfamily Laevapecinae on the basis of the haploid chromosome number 17. Albrecht et al. (2004) tested whether the shell shape of *Burnupia* evolved independently and inferred its position within the Basommatophora. They concluded that the patelliform shell shape evolved at least three times in the Basommatophora, as previously proposed by Hubendick (1978), representing cases of convergent evolution. Currently, *Burnupia* is considered outside the Ancylinae according to Albrecht et al. (2007), who suggested a new “unnamed clade” for this genus. *Burnupia* not only appears to be distinct from the Ancylinae but also from all other representatives of the superfamily Planorboidea (Albrecht et al., 2007). In reference to the distribution of *Burnupia*, it has long been considered endemic to Africa (Basch, 1963; Wright, 1963; Hubendick, 1964; Albrecht et al., 2004), ranging from the highlands of Ethiopia and East Africa, southwards into Zaire, Angola and Zimbabwe, and widespread in South Africa (Walker, 1924; Hubendick, 1964). Subfossil

shells have also been found in now arid parts of Botswana and Namibia (Brown, 1965, 1994). The number of species belonging to the genus is uncertain, with many established based on shell differences alone, but only few may be distinct species (Brown, 1994). *Burnupia* was first reported from South America by Santos (1990), represented by a single species, *Burnupia ingae* Lanzer, 1991, in Brazil and is one of the eight freshwater limpet genera recorded at the moment for the Neotropical region (Santos, 1990, 2003; Lanzer, 1996; Thiengo et al., 2005; Lacerda & Santos, 2011). Lanzer (1991) referred this species to *Burnupia* based on shell apex micro-sculpture with radially arranged punctuations, considered a diagnostic character by Walker (1912) and Hubendick (1964). The current distribution of *B. ingae* includes the type locality, Sombrio Lagoon, Santa Catarina, south and west-central regions of Brazil: Alagoas, Rio Grande do Sul, Espírito Santo and Mato Grosso (Lanzer, 1996; Santos, 2003; Lacerda & Santos, 2011; Fernandez et al., 2014; Fig. 1) and one locality in the north: Pará (Lacerda & Santos, 2011). Herein we provide new information on its shell sculpture and report new records of *Burnupia ingae* in the state of Rio de Janeiro, which represents an expansion of the known distribution of this species.

MATERIALS AND METHODS

Live specimens of *Burnupia ingae* were collected from several localities in the state of Rio de Janeiro by hand collecting from fallen leaves of riparian vegetation and floating vegetation on the banks of streams, rivers and lagoons. The specimens were housed at Malacological Collection at Universidade do Estado do Rio

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FIGS. 1, 2. Maps showing the distribution of *Burnupia ingae*. FIG. 1: Map with watersheds of Brazil (blue lines), drainage and estate division (black lines) showing previous (yellow circles) and new records (red circles) for *Burnupia ingae*. Abbreviations for watersheds: AL, Atlantic East; Am, Amazonas River; AN, Atlantic North Northeast; AS, Atlantic South Southeast; To, Tocantins River; SF, São Francisco River, Ur, Uruguay River; FIG. 2: Mesoregions Map showing in detail the new sites of *B. ingae* of Rio de Janeiro state; detail of the collecting sites in Caiçaras and Juturnaíba lagoons.



de Janeiro (Col. Mol. UERJ 10873, 10982). Occurrence data for *B. ingae* in Brazil were obtained from published scientific literature (Lanzer, 1991, 1996; Lacerda & Santos, 2011; Fernandes et al., 2014).

All shells were measured with digital Vernier calipers (precision 0.5 mm) following Santos (2003) and included TL (total length), H (height), AW (anterior width) and PW (posterior width). The shell sculpture was examined by removing the periostracum from shells using sodium hypochlorite (5%) for a short time period (5–10 minutes depending on shell size). Radulae were extracted from the buccal mass following the methodology of Lanzer (1995) and imaged via scanning electron microscopy JEOL JSMG390LV (Microscopy Laboratory of Museu Nacional, Rio de Janeiro) along with representative shells. Taxonomic identification was determined based on morphological characters, include shell shape, size, teleoconch and protoconch sculpture and muscle scar shape, following Lanzer (1991), and in comparison with type material from Museu de Ciências Naturais (MCN) da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (Holotype: MCN 31020; Paratypes: MCN 31021, MCN 31022, MCN 31023, MCN 31029).

## RESULTS

### Taxonomy

*Burnupia* Walker, 1912

Type species: *Burnupia caffra* (Krauss, 1848)

*Burnupia ingae* Lanzer, 1991  
(Type locality: Brasil, Santa Catarina,  
Lagoa do Sombrio)

*Burnupia ingae* Lanzer, 1991: 712–718, figs. 13–22.

*Burnupia ingae* – Lanzer, 1996: 202; Santos, 2003: 206; Lacerda et al., 2011: 862; Fernandes et al., 2014: 498.

### Material Examined

Brazil: Rio de Janeiro state. Col.Mol. UERJ 10872, Silva Jardim municipality Juturnaíba Lagoon, 22°39'05"S, 42°20'29.3"W, 03/08/2011, Lacerda, LEM; Santos, SB; Miyahira, IC & Carneiro, JB Leg. Col. Mol 10873, Piraí municipality, Caiçaras lagoon, 22°39'29.9"S, 43°51'03.9"W,

28/11/2014, Santos, SB & Ovando, XMC Leg. Col. Mol. 10982, Rio de Janeiro, Piraí municipality, Caiçaras lagoon, 22°39'29.9"S, 43°51'03.9"W, 28/10/2014, Ovando, XMC Leg. Santa Catarina state. MCN 31020, Sombrio, Sombrio Lagoon, 29/04/1981, Lanzer, R & Schwarzbald, A Leg. MCN 31021, Sombrio, Sombrio Lagoon, 29/04/1981, Lanzer, R & Schwarzbald, A Leg. Rio Grande do Sul state. MCN 31022, Osório, do Lessa Lagoon, 11/04/1981, Lanzer, R & Schwarzbald, A Leg. MCN 31023, Tramandaí, Gentil Lagoon, 25/03/1984, Lanzer, R & Chomenko, L Leg. MCN 31029, Palmares do Sul, Cipó Lagoon, 20/01/1982, Lanzer, R & Chomenko, L Leg.

### Habitat and Distribution

Most of the collected specimens were found attached to aquatic vegetation, branches and leaves inside the water. Juturnaíba lagoon has an area of 43 km<sup>2</sup> and is located in Baixadas Mesoregion. Juturnaíba serves as a reservoir that supplies the Lagos region cities (Fig. 2), while Caiçaras lagoon is a small pond (0.05 km<sup>2</sup>) in Sul Fluminense Mesoregion. Juturnaíba lagoon, currently dammed, is surrounded by extensive grasslands and diverse crops, exotic vegetation and remnants of Atlantic Forest, particularly near Poço das Antas Biological Reserve. Caiçaras Lagoon is surrounded by marginal vegetation, mainly exotic almond trees, jackfruits, pines and remnants of Atlantic forest, and aquatic vegetation (e.g., *Typha* sp). However, until recently, the only record for *Burnupia ingae* for the southwest region was from the state of Espírito Santo (Lacerda & Santos, 2011), which corresponds to a small unnamed stream, surrounded by pastures in the locality of São Vicente.

Our records expand the known geographic distribution of this species in the southeastern region (Figs. 1, 2).

The ancyliids *Gundlachia ticaga* (Marcus & Marcus, 1962) and *Ferrissia fragilis* (Tryon, 1863) were found together with *B. ingae*. These ancyliids species have numerous records of occurrences in the state (Lacerda & Santos, 2011, 2015; Thiengo et al., 2005).

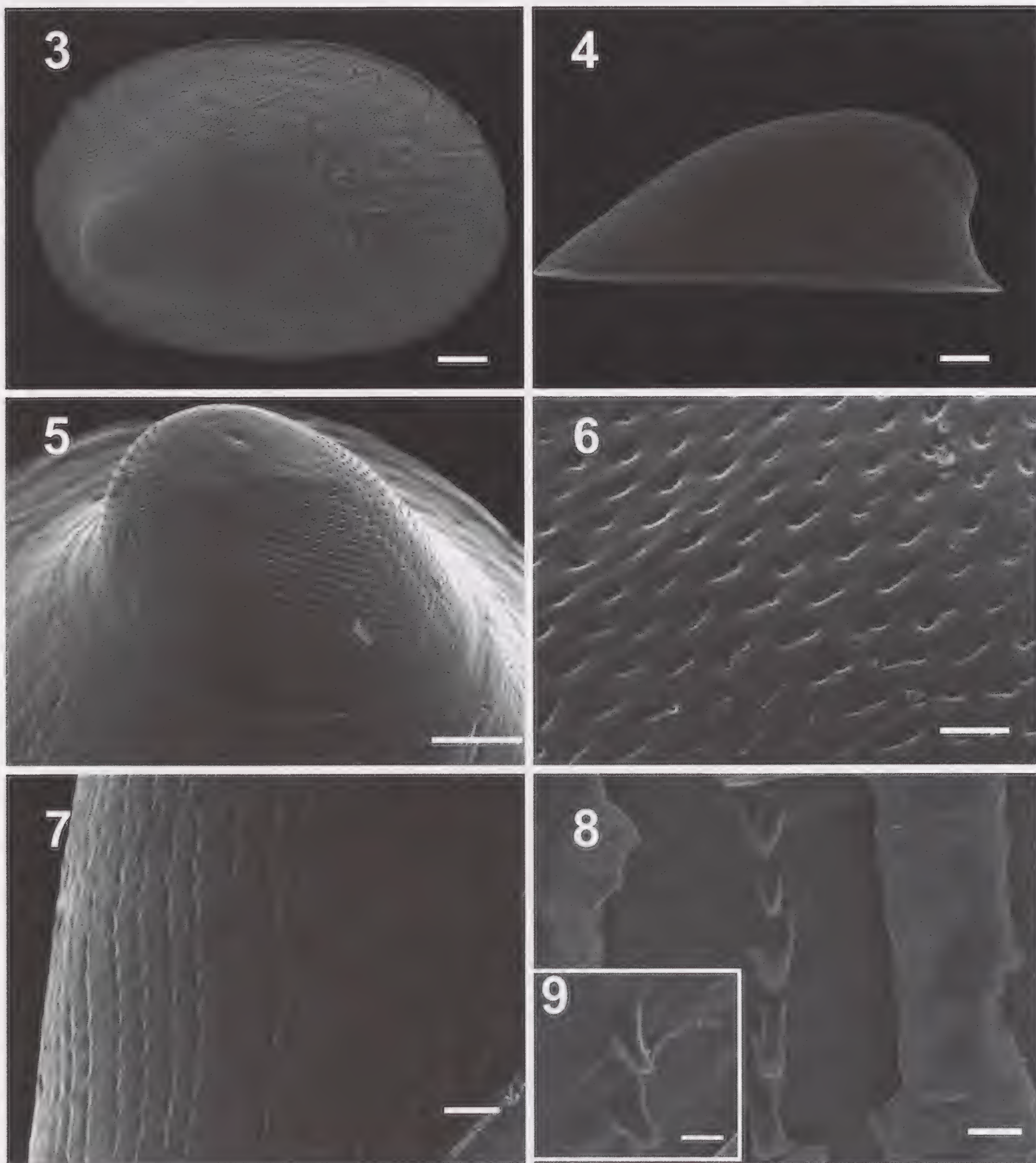
### Description

All specimens studied match well with the original description of *B. ingae* by Lanzer (1991). All specimens lacked pigmentation on the mantle. The shell was circular to oval-shaped, elevated, with rounded obtuse apex located in posterior left side of the shell with



the typical shell apex sculpture (Figs. 3, 4), with right anterior muscle scar longitudinally elongated and the posterior one elongated-oval. Apex microsculpture showed a smooth apical depression followed by pits of irregular

shape and size, regularly arranged in single radial rows (Figs. 5, 6). Teleoconch sculpture formed by dashed grooves, regularly spaced in radial arrangement over the shell surface (Fig. 7). Shell microsculpture with periostracum



FIGS. 3–9. Shell of *Burnupia ingae*. FIG. 3: Dorsal view of shell with periostracum showing the radial periostracal hairs. Scale bar = 200  $\mu$ m; FIG. 4: Lateral view of shell without periostracum showing teleoconch sculpture. Scale bar = 200  $\mu$ m; FIG. 5: Protoconch sculpture with the pits in radial arrangement. Scale bar = 100  $\mu$ m; FIG. 6: Detail of protoconch sculpture showing the shape of pits. Scale bar = 20  $\mu$ m; FIG. 7: Detail of teleoconch sculpture showing dashed grooves, regularly spaced. Scale bar = 50  $\mu$ m; FIGS. 8, 9: Detail of teleoconch sculpture with periostracum showing periostracal hairs. Scale bar = 10  $\mu$ m.



TABLE 1. Mean, range and ratios of measurements from shells for *Burnupia ingae* Lanzer, 1991 from the new localities of occurrence in Rio de Janeiro state, Brazil. Means and standard deviation (mm); n = numbers of shells measured; L total length; W1 anterior width; W2 posterior width; H total height; (W1/L) anterior width/length; (W2/L) posterior width/length; (H/L) height/length; (H/W1) height/ anterior width; (W2/W1) posterior width/ anterior width.

| Measurements |         | Juturnaíba Lagoon<br>(n = 13) | Caiçaras Lagoon<br>(n = 52) |
|--------------|---------|-------------------------------|-----------------------------|
| L            | Minimum | 1.18                          | 1.21                        |
|              | Maximum | 2.36                          | 2.27                        |
|              | Mean    | 1.78 ± 0.39                   | 1.74 ± 0.23                 |
| W1           | Minimum | 0.87                          | 0.79                        |
|              | Maximum | 1.47                          | 1.52                        |
|              | Mean    | 1.19 ± 0.21                   | 1.12 ± 0.14                 |
| W2           | Minimum | 0.60                          | 0.48                        |
|              | Maximum | 1.26                          | 1.42                        |
|              | Mean    | 0.99 ± 0.19                   | 1.00 ± 0.16                 |
| H            | Minimum | 0.36                          | 0.36                        |
|              | Maximum | 0.90                          | 0.89                        |
|              | Mean    | 0.68 ± 0.17                   | 0.67 ± 0.10                 |
| W1/L         | Minimum | 0.60                          | 0.50                        |
|              | Maximum | 0.75                          | 0.82                        |
|              | Mean    | 0.67 ± 0.05                   | 0.64 ± 0.07                 |
| W2/L         | Minimum | 0.46                          | 0.36                        |
|              | Maximum | 0.67                          | 0.73                        |
|              | Mean    | 0.56 ± 0.06                   | 0.57 ± 0.07                 |
| H/L          | Minimum | 0.23                          | 0.27                        |
|              | Maximum | 0.50                          | 0.50                        |
|              | Mean    | 0.38 ± 0.06                   | 0.39 ± 0.05                 |
| H/W1         | Minimum | 0.39                          | 0.36                        |
|              | Maximum | 0.70                          | 0.78                        |
|              | Mean    | 0.56 ± 0.09                   | 0.60 ± 0.08                 |
| W2/W1        | Minimum | 0.65                          | 0.49                        |
|              | Maximum | 0.92                          | 1.00                        |
|              | Mean    | 0.83 ± 0.06                   | 0.89 ± 0.11                 |

showed small periostracal hairs arranged radially, spaced regularly on the over surface of the shell (Fig. 3). Each periostracal hair is short, flat; width irregular and blunt ended (Figs. 8, 9). Shells lengths (L) ranged from 2.36–1.18 mm in Juturnaíba lagoon, while Caiçaras lagoon where slightly smaller, with a mean of 1.74 mm (Table 1). The small size of specimens of *B. ingae* found, rarely reaching 2.3 mm length.

# DISCUSSION

We report the presence of *Burnupia ingae* from the state of Rio de Janeiro for the first time and provide data on a novel morphological character from shell sculpture. We believe that this new character will help in distinguishing *Burnupia ingae* from congenetics. Based on previous records for *B. ingae* from Brazil



(Lanzer, 1991; Fernandez et al., 2014), we noted *B. ingae* is frequently found in lentic environments (e.g., ponds and flooded areas), and it is considered an indicator species for eutrophic conditions from aquatic habitats in southern Brazil (Lanzer & Schäfer, 1987). The environments where *B. ingae* was found, which are similar to that of type locality, indicate that this species prefers lentic waters. In comparison with the type material, the shells of specimens from Lagoa dos Caiçaras were smaller than the holotype and paratype material of *B. ingae*. On the other hand, anterior width (W1) and posterior width (W2) measurements were similar to those reported by Lanzer (1991). At the moment, the maximum value registered for *B. ingae* corresponds to material from Sombrio Lagoon (Santa Catarina state), with 3.0 mm shell length (Lanzer, 1991). The small size of *B. ingae* could explain its absence from other surveys and previously freshwater snail fauna lists. *Burnupia ingae* is smaller than African congeners; Oberholzer & van Eeden (1969) recorded a shell length of 7 mm for *B. mooiensis* (Walker, 1912), and Walker (1924) reported 10 mm shell length for *B. gordonensis* (Melvill & Ponsonby, 1903).

The SEM analyses revealed that the shell apex harbors numerous pits radially arranged, similar to Lanzer's (1991) description and consistent with the diagnostic characters reported by Walker (1912) and Brown (1994) for *Burnupia*. Pits closer to the apical depression were rounded, while the more distal pits have a rectangular shape, but all were arranged in radial rows following the same pattern described by Walker (1912). However, these irregularly shaped pits differ from other *Burnupia* species, such as *B. stenochorias*, in which all the pits are square (Davies-Coleman, 2001). For *Burnupia mooiensis*, Oberholzer & van Eeden (1969) and Connolly (1939) described a different pattern of the pits arrangement in the radial rows, the first four or five pits have a single disposition (one behind the other) in each row, but thereafter they are arranged with two pits per row. Microscopic analyses also revealed that "small prominences on the periostracum surface" Lanzer (1991) are tiny periostracal hairs in a radial arrangement. The presence of periostracal hairs is currently used as a diagnostic feature for the genus *Uncancylus* (Santos, 2003; Ovando et al., 2014), but has not been previously reported for any *Burnupia* spp. The periostracal hairs of *B. ingae* are not similar in shape or size to those of *U. concentricus*, the latter being thin and sharp and the former short, flat and blunt ended. Pilsbry

(1920) suggested that *Uncancylus* and *Burnupia* are closely related. However, haired shells occur in several species of gastropods, suggesting that those features have evolved multiple times independently (Pfenninger et al., 2005). Based on this, the presence of periostracal hairs could be a character evolved independently in both genera.

The new records reported herein extend the geographic distribution of *B. ingae* to southeast Brazil, and analyses of these samples further develop our understanding of the morphology and distribution of this freshwater species in the country and their relationships to other limpet groups. Additional studies are required to fully understand the distributional limits and affinities among the South American and African species of *Burnupia*. Such studies must take an integrative approach unifying morphological and molecular studies to contribute to systematic of freshwater limpets broadly.

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## OBSERVATIONS ON GROWTH RATES AND MATURITY IN AN INTRODUCED POPULATION OF THE ROMAN SNAIL (*HELIX POMATIA* LINNAEUS, 1758) AT A SEMI-NATURAL SITE WITH NO NATURAL POPULATION

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### INTRODUCTION

*Helix pomatia* Linnaeus, 1758, the Roman snail, is widely exploited for food in Europe. Over-exploitation has led to protective measures laid down in the European Union Habitats Directive (European Community Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC). In Poland, the implementation of this directive has involved passive protection by means of closed seasons for collecting, minimum size limits and annual rotation of areas in which collecting is permitted (Dyduch-Falniowska et al., 2001). The size limit (minimum shell diameter of 30 mm) has not changed for several decades.

*Helix pomatia* has relatively slow reproductive and maturation rates (Ligaszewski et al., 2014). Efforts have been made to improve these under controlled conditions (Jeppensen, 1976; Gomot, 1990; Chmielewski, 2005). In experiments at the National Research Institute of Animal Production in Balice, Poland, mature *H. pomatia* taken from the wild and kept in greenhouses reproduced successfully, producing large numbers of hatchlings both in autumn and after the winter hibernation (Ligaszewski et al., 2007). While rearing snails in such conditions over the whole of their life cycle (eggs to harvested adults) is expensive, the release of juveniles into apparently suitable habitats might increase the number of natural populations and serve to secure the snail's future in the face of exploitation.

This study thus set out to determine the fate of juveniles reared in greenhouses and released into a semi-natural, synanthropic site in which the snail was absent. A target area was modified to provide good starting conditions, and the growth rate and dispersal of the introduced juveniles studied over the period 2011–2015. In particular, the study aimed to

determine the time taken to reach the legally harvestable size and the extent to which the release site was able to sustain a breeding population.

### MATERIAL AND METHODS

#### The Site

In the early spring of 2011, a release site was established on the edge of the Będkowska valley near Kraków. No natural populations of the Roman snail had been found in the years preceding the study. The site (Fig. 1), previously subject to farming activities, lies on calcareous soil. A portion of the site was ploughed and reseeded with a mixture of fodder plants composed predominantly of white clover (*Trifolium repens*), red clover (*Trifolium pratense*), winter bird rape (*Brassica rapa* x *Brassica rapa* subsp. *Chinensis*), radish (*Raphanus sativus*) and carrot (*Daucus carota*). These crops were sown to improve trophic conditions on the site, enabling the newly created, naturalized experimental population to survive during the first years of the experiment. This part of the site, where the snails were to be released, was then supplied with stone and wooden hiding places for the snails.

Although the vegetation in this portion of the site changed in subsequent years, the balance of grasses, legumes and other dicotyledons did not vary much over the period of study. Over the course of the study many snails moved out of the release area into other parts of the site (Fig. 1). An adjacent area containing black currant (*Ribes nigrum*) and hazelnut shrubs (*Corylus avellana*) proved attractive for adult snails seeking shelter and egg laying sites. Other areas were reseeded with clover.

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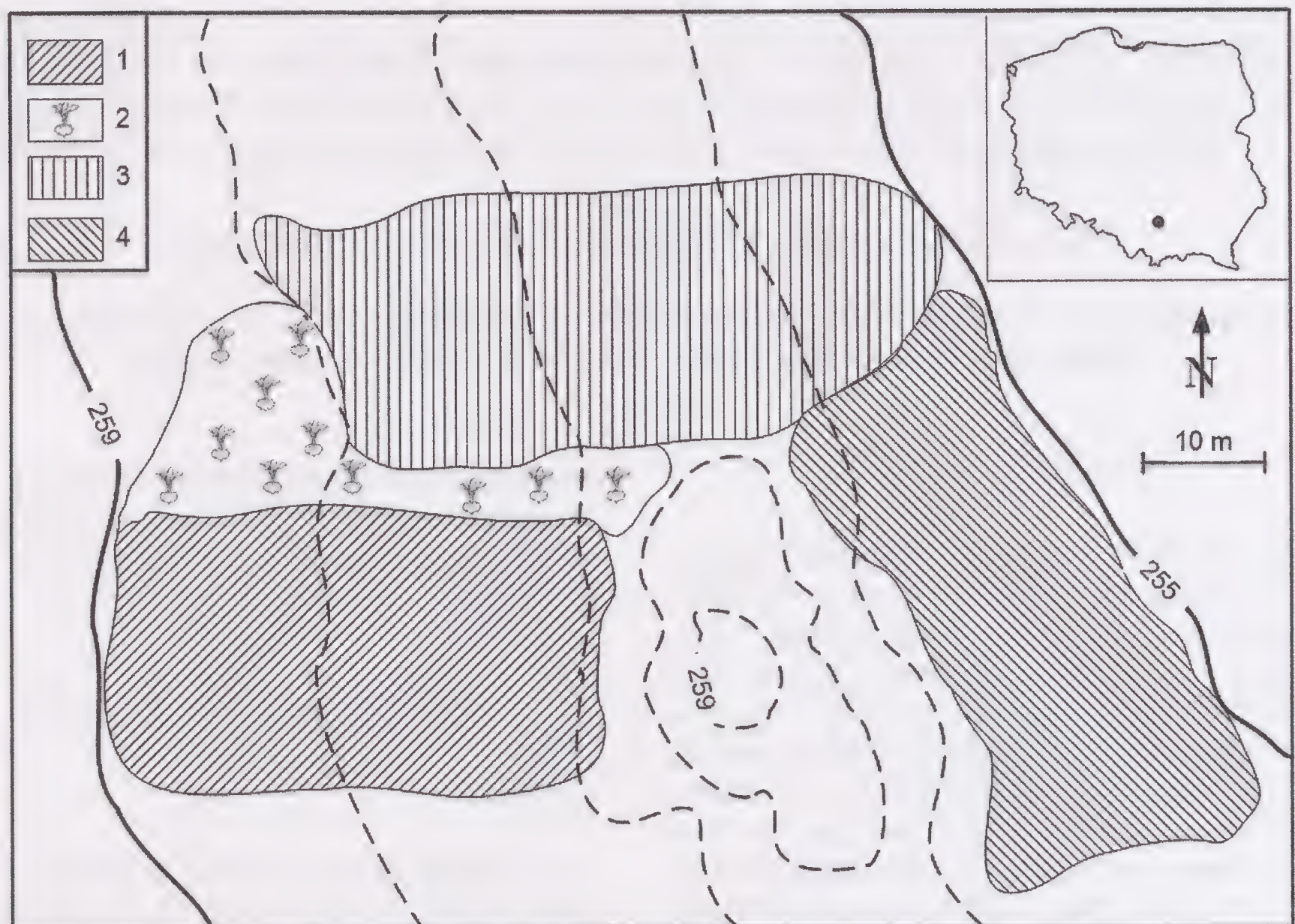


FIG. 1. Land survey and height map. Legend: 1. Sampling area in 2011–2012. In 2011, snails were introduced to the area with stone piles, sown with fodder plants. Area about 999 m<sup>2</sup>; 2. The first reproduction area of mature Roman snails in 2012. Horticulture, wild black currant shrubs. Area about 350 m<sup>2</sup>; 3. Sampling area in 2013–2014. Direction of the first expansion and reproduction of the marked snails. Hazelnut shrubs, sown white clover, Sample collection in 2015. Area about 1050 m<sup>2</sup>; 4. Area of the second phase of expansion and reproduction of mature snails. Wild black currant field, white clover. Area about 970 m<sup>2</sup>.

#### Source and Treatment of Released Snails

The snails that were the parents of those released came from a natural population at Balice, near Krakow. The mean shell diameter of these snails was 33.8 mm (SD,  $\pm 1.8$  mm, range 30.0–39.2 mm) and a wet body weight (including shell) of 21.2 g (SD  $\pm 3.3$  g, range 13.9–32.8 g). These snails were kept in an unheated greenhouse. Eggs laid in 2010 by these snails hatched and the small juveniles emerging were left in the greenhouse until May 2011, having had one season of growth and one of hibernation.

In May 2011, 3,000 of these juveniles were released in an area of about 1,000 m<sup>2</sup> in that part of the experimental site that had been prepared by reseeded and the provision of shelter, giving an initial density of 3 snail m<sup>-2</sup> (Fig. 1). Before release, each snail was marked with organic wood varnish, the chips of which remained visible under a magnifying glass in most of the snails until 2014.

#### Sampling

Between May 2011 and May 2015 snails were sampled at irregular intervals within the active season (Table 1). Sampling was carried out when conditions were favourable for activity: early in the morning after rain, but in sunny and warm conditions. Periods of drought limited sampling in some years, most strongly in 2013. In 2015 the possibility of confusion between the released snails and their newly adult offspring was possible, as some marks had disappeared. Hence, a single collection was made in May 2015, when it was possible to separate them on the basis of shell wear and other signs of maturity (Ligaszewski et al., 2014). On each sampling occasion, the same person searched for snails for one hour in an area of about 1,000 m<sup>2</sup>. This protocol was designed to minimize damage and disturbance.

In 2011 and 2012 many snails remained in the release area, but in later years it became apparent that most had moved to adjacent



TABLE 1. The numbers, age and measurements of snails captured on each sampling occasion during the study. The figures for May 2011 refer to a random sample of 10% of those released at that time.

| Sampling date | Number of snails | Nominal age (months) | Mean body wt (g) | Standard error | Mean shell diameter (mm) | Standard error |
|---------------|------------------|----------------------|------------------|----------------|--------------------------|----------------|
| May 2011      | 299              | 11.0                 | 5.92             | 0.19           | 21.00                    | 0.23           |
| July 2011     | 127              | 12.5                 | 9.11             | 0.32           | 25.17                    | 0.30           |
| Sept. 2011    | 159              | 14.5                 | 10.46            | 0.33           | 25.05                    | 0.27           |
| May 2012      | 196              | 22.5                 | 13.98            | 0.31           | 29.39                    | 0.19           |
| June 2012     | 205              | 23.5                 | 20.88            | 0.35           | 31.23                    | 0.15           |
| July 2013     | 75               | 36.5                 | 18.06            | 0.26           | 31.73                    | 0.17           |
| June 2014     | 114              | 48.0                 | 19.58            | 0.33           | 31.00                    | 0.18           |
| July 2014     | 118              | 49.0                 | 19.63            | 0.34           | 32.17                    | 0.19           |
| May 2015      | 160              | 59.0                 | 18.70            | 0.19           | 33.02                    | 0.11           |

areas (Fig. 1). The areas chosen for sampling were therefore changed for 2013 and 2014 and again in 2015, but were always restricted to about 1,000 m<sup>2</sup>.  
Snails collected on each occasion were weighed and their shell diameter measured.

They were then returned immediately to the field. In tables, the age of the snails is given in months since the nominal time of hatching in the greenhouse (the end of June 2010) where it was following by rearing and hibernating till the end of May 2011.

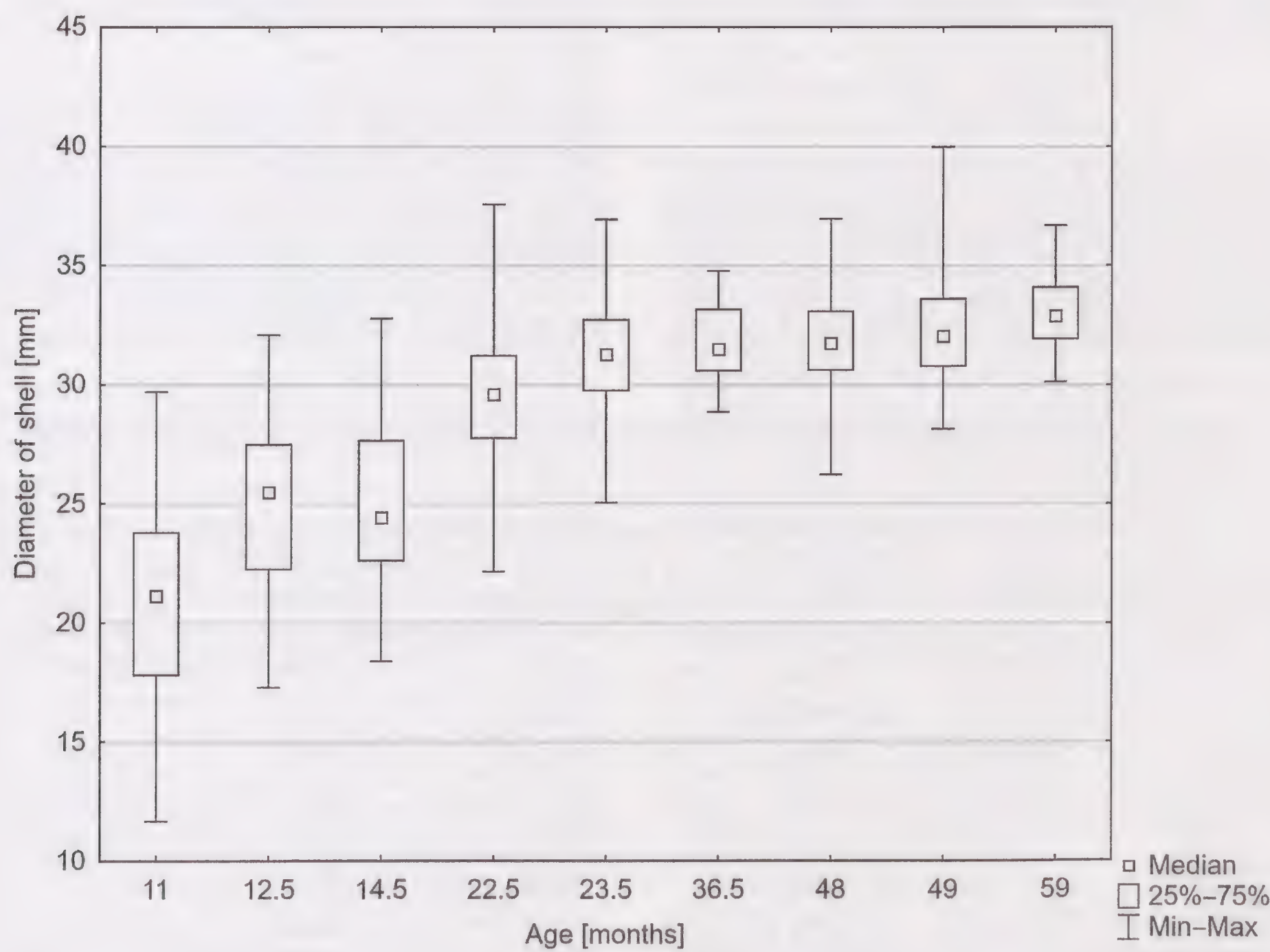


FIG. 2. Median for the shell diameter of *Helix pomatia* snails in consecutive seasonal samples.



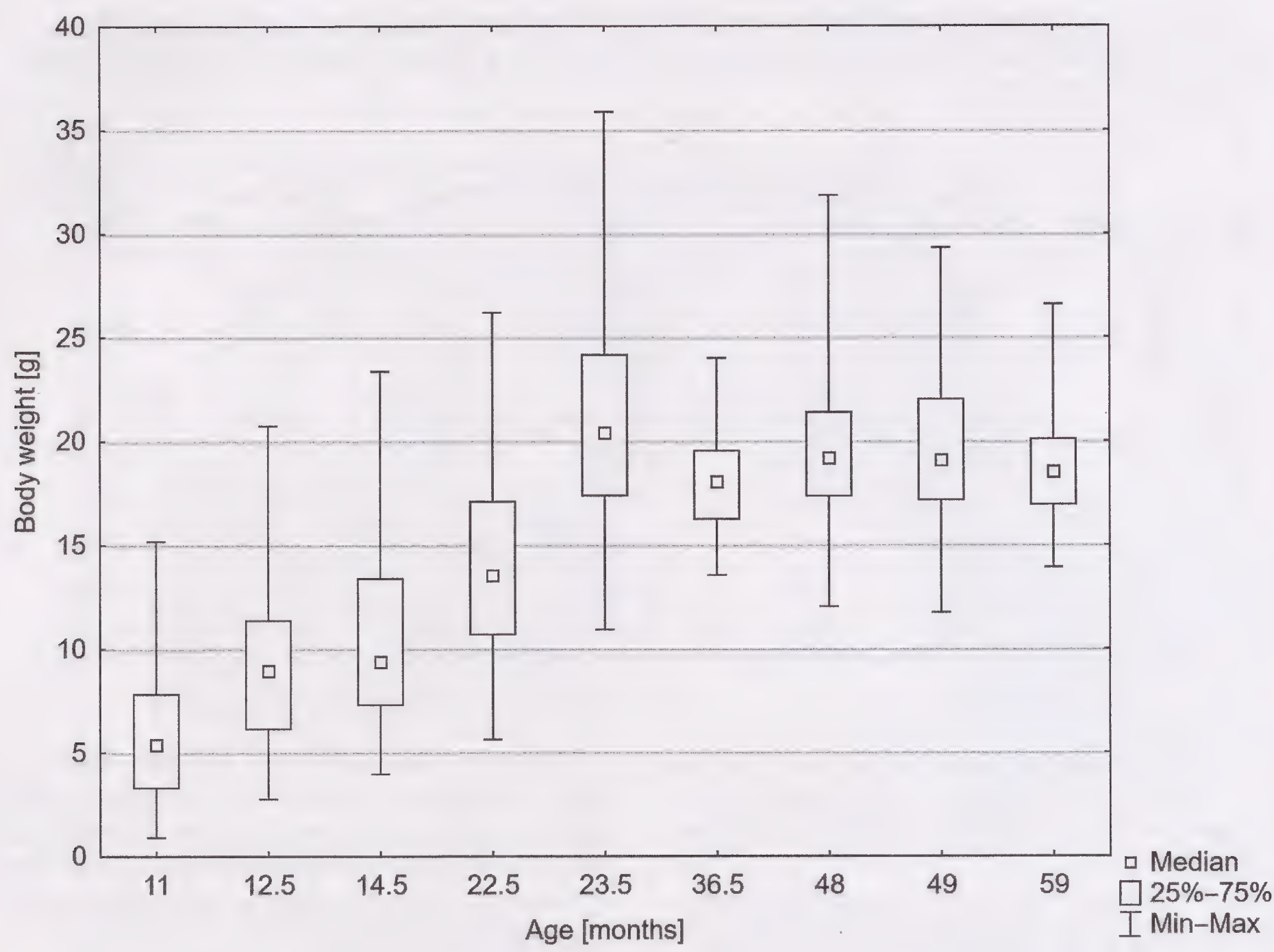


FIG. 3. Median for the body weight of *Helix pomatia* snails in consecutive seasonal samples.

RESULTS

The numbers and measurements of snails captured on each occasion are shown in Table 1. Both the body weight and shell diameter increased over time (Figs. 2, 3). In both cases, growth is rapid up to around two years of age.

Body weight shows fluctuations and even some declines thereafter, but shell diameter continues to increase very slowly. In June 2012, some snails were mature enough to start laying eggs around the perimeter of the original release area. In later years, reproduction was also observed in areas to which the snails had moved.

TABLE 2. Characteristics of *Helix pomatia* snails with shell diameter exceeding the legal size limit of 30 mm.

| Age group | Age (months) | Sampling time | Proportion in sample (snails; %) | Shell diameter (mm snail <sup>-1</sup> ) | Body weight (g snail <sup>-1</sup> ) |
|-----------|--------------|---------------|----------------------------------|------------------------------------------|--------------------------------------|
| 1+        | 12.5         | July          | 8.7                              | 31.4                                     | 16.4                                 |
|           | 14.5         | September     | 8.2                              | 33.9                                     | 20.4                                 |
| 2+        | 22.5         | May           | 41.3                             | 31.6                                     | 17.6                                 |
|           | 23.5         | June          | 72.7                             | 32.1                                     | 22.7                                 |
| 3+        | 36.5         | July          | 89.7                             | 32.0                                     | 18.4                                 |
| 4+        | 48.0         | June          | 86.0                             | 32.3                                     | 20.3                                 |
|           | 49.0         | July          | 86.4                             | 32.7                                     | 20.4                                 |
| 5+        | 59.0         | May           | 99.7                             | 33.0                                     | 18.6                                 |



By May 2012, just before first breeding, more than 40% of sampled snails exceeded the minimum shell diameter (30 mm) required for legal harvesting (Table 2), and by the end of the experiment nearly all snails exceeded this diameter. It is worth noting that a few snails had reached 30 mm diameter even in the second year of life. The mean diameter of snails on the last sampling occasion (33.02 mm) was significantly less than those of their parents collected from the wild (33.78 mm), but the difference is nevertheless small.

## DISCUSSION

Our experiment shows that release of one-year-old juvenile *H. pomatia* into an unoccupied site can result in successful growth and reproduction. Although the initial release site was prepared to give good conditions for feeding and shelter, the snails spread and reproduced in adjacent areas that were not treated, although these areas underwent changes associated with agricultural and horticultural activity. Our methods did not enable us to estimate mortality, but the ability to find similar numbers of snails per unit effort and area except in drought conditions suggests that after any initial losses it was not great. The spread, over an area far larger than the standard sampling plot, and the evidence of successful reproduction indicate that the area is able to sustain a population over the medium to long term. Previous absence would appear to be a product of chance and the combination of habitat changes over time relative to the powers of dispersal of the snail.

The growth and maturation of the introduced snails was rapid, with evidence of breeding only two years after hatching. The fact that the shell size of almost all mature snails exceeded the legal collecting limit by the end of the study also suggests that there were no serious impediments to growth. Snails maturing in the study site were very similar in size to those in the originating natural population. The size of adult snails is related to the size of their hatchlings at two weeks of age (Gołab & Lipińska, 2009). Thus, there is no evidence that snails developing in the experimental site were at any disadvantage relative to the natural habitat of their parents. However, our evidence suggests that the time taken to attain adult size and condition varies considerably among members of the same cohort. We have no data from natural populations to compare.

Body weight declines seen after two years of life may reflect the loss of mass due to egg laying. An earlier study on reproductive intensity of *Helix pomatia* snails from a natural population found that the average weight of an egg clutch laid in June was 30% of the body weight of marked breeding snails, while in July this value was only 18% of the body weight of breeding snails that produced eggs for the second and third time during the season (Ligaszewski et al., 2007). Drought conditions may also have contributed to fluctuations in body mass.

The site of release and expansion was in private hands and therefore not available to collectors. Apart from collecting, there are other sources of mortality that might affect the persistence of a newly established population. The vertebrate predators most often recorded are mice and birds. According to Rosin et al. (2011), under natural conditions the primary predator for younger and smaller *Helix pomatia* snails that are secretive in habit are mice, while birds tend to attack large, mature, and more active specimens. Although our naturalized population suffered no evident losses (gnawed shells) from mice, thrushes were observed to crush the shells of mature *H. pomatia* snails on stones during the last two years of the study. However, the magnitude of losses caused by animals was difficult to estimate over the large area into which the snails had spread.

Indeed, a significant feature of our study was the observation that as snails matured they moved to other parts of the study site. Mature *H. pomatia* in our introduced population began to move in late spring 2012 from the centre to the edge of the research site. During 2014–2015, the snails made increasingly distant excursions from the original research site, to find shelter under tall hazels and black currant plantation, in areas grown with white clover and in vegetable plantations. Because vegetation changed during the study, we cannot be sure whether these movements were related to detecting suitable food or to finding sites suitable for egg laying. During the last two years of sampling the original release site held only young snails that had hatched on the site. While this indicates that at least in 2013 some of the snails introduced in 2011 were still laying eggs there, it is clear that mature adults had moved elsewhere.

These relatively long distance movements and the choice of different areas for feeding, growth and reproduction appear to be common in this species. Nica et al. (2012) showed that



adult *H. pomatia* often made long excursions to find proper soil and microclimatic conditions for egg laying. As stated by Klimas et al. (2012), the white clover is a favorite food plant of *H. pomatia*: the growth rate of immature snails depended on the quality of its leaves (Ledergeber et al., 1998). Rather than moving seasonally, young *Helix pomatia* snails were sedentary in the area in which they hatched from eggs (Lind, 1990). He stated then that mature snails migrated for one to four weeks to tree-covered areas in search of new areas to lay eggs or to look for a more food-rich environment than in the area where they were reared.

Our study has shown that, at least with some preparatory work, an introduction of juvenile *H. pomatia* can be successful. The behaviour of the snails, however, shows that quite a large area with a variety of vegetation types may be needed. Changes in occupied sites may well influence the distribution of snails within it, and there may be differences between parts that provide feeding or breeding conditions. Estimating the extent and density of populations with any degree of accuracy is correspondingly challenging.

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## PHYSA ACUTA DRAPARNAUD, 1805 SHOULD BE TREATED AS A NATIVE OF NORTH AMERICA, NOT EUROPE

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### ABSTRACT

*Physa acuta* (Gastropoda: Heterobranchia: Physidae) is a freshwater snail commonly found in North American rivers, streams and ponds. Despite its widespread distribution across the United States, it is generally regarded as an invasive species. As a result, *P. acuta* receives no attention during conservation management inventories. However, data suggest that *P. acuta* may be a native to North America rather than to Europe, where it was first described. First, the fossil record in Europe lacks *P. acuta*, whereas North America is home to numerous fossils of members of the *acuta* species group. Second, breeding studies among *P. acuta* and North American taxa from the *acuta* species group show no evidence of pre- or postzygotic isolation. Third, investigations of reproductive anatomy between *P. acuta* and other nominal species of the *acuta* species group are indistinguishable, leading investigators to synonymize taxa. Finally, phylogenetic data do not support the distinction of *P. acuta* from its North American congeners of the same species group. Together, these data support our case that *P. acuta* is a North American native.

Key words: *Physa*, *acuta*, gastropods, indigenous, native, non-native.

### INTRODUCTION

*Physa acuta* Draparnaud, 1805, was first described from the Garonne River in France and long considered to be indigenous to Europe (Te, 1978; Burch & Tottenham, 1980; Burch, 1982, 1988). Reports that the species may actually be native to North America first appeared in 2002 when Dillon et al. (2002) proposed that the species was not reproductively isolated from *P. heterostropha* (Say, 1817) and *P. integra* (Haldeman, 1841), and Anderson (2003) found no anatomical differences between it and the North American native *P. heterostropha*. Johnson et al. (2013), in their examination of the conservation status of native North American gastropods, did not include *P. acuta* in their account because they considered it a non-native (Johnson et al. 2013; P. D. Johnson, personal communication). It is important to establish whether the species is native or non-native because management strategies for it will differ greatly depending on whether it is an invasive species occupying various habitats and expanding its range or a native that may be declining in certain parts of its distribution and require conservation efforts.

Here, we synthesize available fossil, reproductive, anatomical and phylogenetic evidence to make a case that *P. acuta* is indeed a native of North America.

### FOSSIL EVIDENCE

Interpreting the physid fossil record is challenging. As the range of variation and classification of extant species is not agreed upon, confidently assigning fossils to a particular group is often difficult. Some supposed physids have been reidentified as sinistral lymnaeids (Pierce, 1996). There is also some risk of mistaking shells only a century or two old for fossils. Nevertheless, preservation and abundance is sometimes quite good for fossil non-marine mollusks, providing large enough samples to determine the level of variation.

We have not located any records of fossil *P. acuta* in Europe. For example, Kennard & Woodward (1926) cited *P. acuta* as an invasive in Britain, primarily known from gardens and not reported from the Pleistocene. Most European fossil physids are assigned to *Physa* s.s. (in the Pleistocene, often *P. fontinalis*

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(Linnaeus, 1758)) or *Aplexa* (Pacaud & Le Renard, 1995; Harzhauser & Mandic, 2008; Preece, 2010). Conversely, *P. acuta* (including *P. integra*, *P. virgata* (Gould, 1855), *P. sayii* (Kirtland, 1838) and *P. heterostropha*) is widely reported as a fossil in North America (Taylor, 1966; La Rocque 1968; Taylor, 1975; Czaja et al., 2014). This strongly supports a North American origin for *P. acuta*. As *P. acuta* ranges only north to southern Canada, it seems unlikely to have crossed the Bering land bridge in the Pleistocene.

### BREEDING STUDIES

Mating studies between *Physa acuta*, *P. integra* and *P. heterostropha* have also suggested that the original description of *P. acuta* as a native of France is mistaken. Dillon et al. (2002) assessed a variety of prezygotic and postzygotic isolation factors between these species. The prezygotic factors, which Dillon et al. (2002) described as either a reduction of fertilization or fecundity, were not seen in any intercrosses between separate populations. Furthermore, there seemed to be no reduction in viability or fertility in intercrosses involving French *P. acuta* and their North American counterparts, which would indicate postzygotic reproductive isolation if present. The F1 offspring were not only viable, but capable of producing viable F2 offspring themselves without issue. The evidence presented by Dillon et al. (2002) certainly suggests that *P. acuta*, *P. heterostropha* and *P. integra* are conspecific. Similar studies between *P. acuta* and North American *P. virgata* have also supported the synonymy of these species (Dillon et al., 2005). These results support the notion that all of these species are united as a single entity under the biological species concept. Phylogenetic evidence lends strong support to the fuzzy boundaries between previously described species, further supporting their synonymy (Wethington & Lydeard, 2007).

Dillon et al. (2002) also found an astonishing amount of genetic variation within wild-caught populations of physids. Although no significant differences were found that would have suggested reproductive isolation between populations, life-history characters varied between individual mating pairs. Although the researchers believed this to be the product of true genetic variation among populations, it does not seem that this genetic variation indicates a true species boundary.

At present, the populations of *P. acuta* in North America seem to have more genetic variety than those found in other areas, most notably Europe (Dillon et al., 2002). In areas outside of North America, the diversity within populations, particularly morphological diversity, is drastically reduced and indicative of invasive populations (Dillon et al., 2002).

### ANATOMICAL EVIDENCE

The reproductive anatomy of physids has proven useful for examining their taxonomy and phylogeny (e.g., Te, 1978; Wethington & Lydeard, 2007). Paraense & Pointier (2003) examined the reproductive anatomy of topotypic specimens of *P. acuta* from the Garonne River basin and additional samples from near the French cities of Montpellier and Perpignan and compared them to topotypic *P. cubensis* of the New World. The two nominal species were indistinguishable, leading the authors to synonymize them under the name *P. acuta*. Anderson (2003), examining the geographic origins of physids in Britain and Ireland, synonymized *P. heterostropha*, a native of the eastern and southeastern United States, with *P. acuta* based on anatomical evidence and proposed that the species was introduced to Europe from North America. Together these data support the notion that *P. acuta* is a North American native.

### PHYLOGENETIC EVIDENCE

Wethington & Lydeard (2007) examined the systematics of the family Physidae using mitochondrial 16S rRNA and cytochrome c oxidase subunit I genes. They found that there was no evidence for distinct monophyly of the following nominal species within the so-called "penial morphology c complex" (Te, 1978): *Physa acuta*, *P. cubensis* Pfeiffer, 1839, *P. heterostropha*, *P. integra* and *P. virgata*. All were sampled at or near their type localities, including for *P. acuta* in France and the Netherlands. If *P. acuta* were indigenous to Europe, one would have expected it to be monophyletic and genetically differentiated from North American species, perhaps not unlike European and North American lymnaeid species (Remigio & Blair, 1997). Given the lack of monophyly, genetic differentiation, and the fact that it was the earliest available name, Wethington & Lydeard (2007) proposed that only *P. acuta*



be recognized from the aforementioned list of nominal species and that the others be synonymized with it. Given that so many physid species were discovered and described from North America during the early to mid-1800s, it seems more parsimonious to presume that *P. acuta* is native to North America and was subsequently introduced to France and described than that it was introduced multiple times into North America throughout the United States, followed by a plethora of new species being described.

### CONCLUSION

Together, the evidence supports the hypothesis that *P. acuta* is indigenous to North America. It is likely that Draparnaud described *P. acuta* thinking it was new to France. Given other common European species, such as *Radix peregra* (Müller, 1774) or *P. fontinalis*, were described as early as 1760 and *P. acuta* not until 1805 suggests that it may not have been in Europe at this time (Bousset et al., 2014). This is not unprecedented. Despite the genus name *Hawaiiia* having been established for a supposedly Hawaiian species, *Helix kawaiensis* Reeve, 1854, this species is now considered a junior synonym of *Helix minuscula* Binney, 1841, which is not an indigenous species in the Hawaiian Islands but has been introduced (Cowie, 1997). More recently, Ng et al. (2015) showed through morphological and DNA barcoding that both *Physastra sumatrana* (Martens, 1897) and *Stenophysa spathidophallus* Taylor, 2003, in Singapore are actually both introduced *P. acuta*. *Physa acuta* probably was introduced to Europe during the cotton trade between France and the United States in the 18<sup>th</sup> century and subsequently spread through the Mediterranean regions and then more slowly into northern Europe, Africa, Asia and Australia (Oscoz et al., 2010). As a North American native, its conservation status is stable.

### ACKNOWLEDGMENTS

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## LETTER FROM THE EDITOR







LETTER FROM THE EDITOR

With this letter I announce my resignation as Editor-in-Chief of *Malacologia*. After 42 years of editing the journal, it is high time that I pass the work on to another.

I was a graduate student in the Museum of Zoology at the University of Michigan in 1960 when one of my mentors there, Professor Jack Burch, began to organize the beginnings of the journal. With generous help from a National Science Foundation grant made possible by a program officer there, J Frances Allen (for whom the Institute of Malacology outstanding student publication award is dedicated), the first issue of the journal was published in 1962. The journal is governed by the Institute of Malacology with its eight-person Board of Directors.

Soon after my return to the United States from a position and laboratories in Japan in 1970 to take a curatorship at the Academy of Natural Sciences of Philadelphia, Dr. Burch made a visit to ANSP and asked if my colleague Dr. Robert Robertson and I would take over editorship of *Malacologia*. We agreed and a few years later I became Editor-in-Chief.

It is a pleasure to announce that my successor is Charles Lydeard, Professor and Chair, Department of Biological Sciences, Western Illinois University, Waggoner Hall 316, 1 University Circle, Macomb, Illinois, U.S.A. 61455-1390. Tel: 309-298-2408; Fax: 309-298-2270. Email for *Malacologia*: clydeardmalac@gmail.com. Chuck will guide the production of vol. 60, to be published in 2017. I am in the process of finishing acceptances of papers of 59(2) to be published in mid to late 2016. Please send all submissions of manuscripts to Chuck starting immediately.

The success of the journal can be attributed to general policies and to the people who re-

ally did the work of getting papers to press. As for policies, the journal has benefitted greatly from being willing to publish papers of any length, to insist on having all the data on which a paper was based, to using reviewers world-wide as long as they were in the top 10% of their field, and to publishing irregularly, that is, not being bound to a quarterly schedule. I have been blessed with superb colleagues. I owe great debts of gratitude to the following: Eugene Coan, who has done the hard work of copy editing of manuscripts since 1989; Caryl Hesterman, who has managed the business affairs of the journal for as long as I have been Editor-in-Chief, doing the invoicing, keeping the books, doing the banking and preparing financial reports; Professor Thomas Wilke has handled graphics editing and whose insistence on excellence of product has made *Malacologia* a journal of highest graphics excellence (he who designed the current cover); Dr. Claudia Wilke has done the page set up for the journal and the indexing, making the journal printer-ready. Tom and Claudia have spent endless hours re-doing graphics and tables to make them fit for international consumption. I am happy that these staff stalwarts have all agreed to stay on in their respective roles.

While most certainly, the success of the journal can be attributed in largest measure to the more than 150 persons who have reviewed manuscripts for the journal over the years, the success of the journal builds on the research contributions of scholars throughout the world. Eugene Coan was so kind as to compile a list of countries of origin for papers published to date in *Malacologia* (Table 1). To all, I give my deepest thanks and gratitude.

George M. Davis  
Editor-In-Chief/*Malacologia*  
21 January 2016

TABLE 1. Non-U.S.A. countries represented by first authors in *Malacologia* 1(1)–59(1). The list includes long and short papers, but not abstracts or symposia introductions. It also includes long, substantive Letters to the Editor. Some authors have changed country, some more than once. The early years were dominated by Europe because of inclusion of European meeting compilations. In later years, the rise of South America, particularly Argentina, is remarkable. It is most assuredly an international journal, with some 846 papers from other countries in contrast to about 525 from the U.S.A.



| Country                                                  | Number of papers |
|----------------------------------------------------------|------------------|
| United Kingdom [England/Scotland/Wales/Northern Ireland] | 134              |
| France                                                   | 108              |
| Argentina                                                | 68               |
| Germany                                                  | 58               |
| Italy                                                    | 41               |
| Spain                                                    | 36               |
| Netherlands                                              | 33               |
| Canada                                                   | 31               |
| Brazil                                                   | 28               |
| Russia [incl. USSR]                                      | 25               |
| Australia                                                | 23               |
| Austria                                                  | 17               |
| China [incl. Hong Kong with 11; Taiwan is below]         | 16               |
| South Africa                                             | 15               |
| Japan                                                    | 14               |
| Poland                                                   | 14               |
| Greece                                                   | 14               |
| Hungary                                                  | 13               |
| India                                                    | 13               |
| Denmark                                                  | 12               |
| Egypt [U.A.R.]                                           | 12               |
| Switzerland                                              | 12               |
| Belgium                                                  | 11               |
| Mexico                                                   | 9                |
| Nigeria                                                  | 9                |
| Czech Republic                                           | 8                |
| Korea                                                    | 7                |
| Norway                                                   | 7                |
| Portugal                                                 | 7                |
| Israel                                                   | 5                |
| New Zealand                                              | 5                |
| "Yugoslavia"                                             | 5                |
| Chile                                                    | 4                |
| Romania                                                  | 4                |
| Thailand                                                 | 4                |
| Ireland                                                  | 3                |
| Algeria                                                  | 2                |
| Finland                                                  | 2                |
| Rhodesia                                                 | 2                |
| Taiwan                                                   | 2                |
| Turkey                                                   | 2                |
| Ukraine                                                  | 2                |
| Croatia                                                  | 1                |
| Fiji                                                     | 1                |
| Ghana                                                    | 1                |
| Jordan                                                   | 1                |
| Liberia                                                  | 1                |
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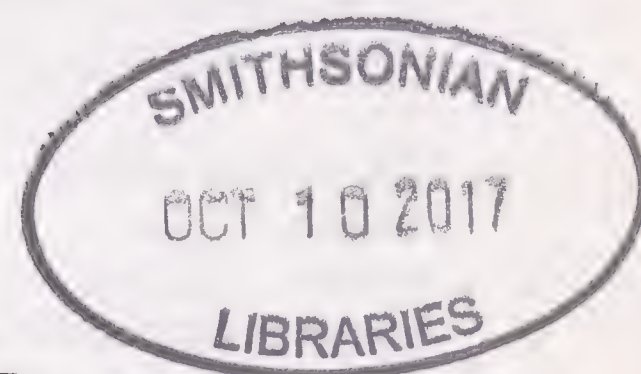
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THE LIFE AND WORK OF RUDOLPH AMANDUS PHILIPPI  
(1808–1904)

Alan R. Kabat<sup>1</sup> & Eugene V. Coan<sup>2</sup>

ABSTRACT

This paper provides a biography of Rudolph Amandus Philippi (1808–1904), emphasizing his malacological research and his contributions to the natural history of Chile. Philippi is one of the most important, yet overlooked malacologists of the 19th century. He authored significant publications on the Recent and fossil molluscs of Sicily; the Oligocene fossil molluscs of northern Germany; the Jurassic to Recent molluscs of Chile, and marine molluscs from around the world. Philippi was also an instrumental contributor to both the *Zeitschrift für Malakozoologie* and the second edition of the *Systematisches Conchylien-Cabinet*, and he founded the *Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien*. In a companion paper (Coan & Kabat, 2017), we provide an annotated catalog of the 2,528 species, 40 genera and 3 families that he described in the Mollusca, and a full bibliography, with collations, of Philippi’s numerous malacological publications.

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INTRODUCTION & BIOGRAPHICAL  
SOURCES

Philippi is probably the least well-known of the major 19th century malacologists and paleontologists, even though his general life has been documented in a wide range of biographical and autobiographical sources. This present-day knowledge gap probably arises from the fact that Philippi was such a polymath, publishing widely on plants, insects, other invertebrates, vertebrates, and even

archaeology. Even though Philippi was one of the most prolific malacologists in terms of the number of his publications and new taxa, his life is poorly documented in the malacological literature – there was only one short obituary of him in any malacological serial (Kobelt, 1904), and the otherwise detailed history of conchology by Dance (1986: 139, 194, 222) devotes only five short sentences to him. Hence, we provide a summary of the key biographical sources for Philippi’s life. While Philippi was in the last decade of his life, he published several autobiographical essays that focused on his travels in Europe and his early years in Chile (Philippi, 1895, 1898, 1901a, 1902, 1903, 1904). More remarkably – and perhaps unique among 19th century malacologists – Philippi prepared an autobiography in 1897 to 1898, *Mein Leben: Meine Lebensbeschreibung (nur für meine Kinder)* [*My life: my autobiography (only for my children)*]. The first 20 or so pages are apparently handwritten by Philippi himself in German, in a very cramped script; the remaining several hundred pages were dictated to his assistant, Bernhard Gotschlich, who transcribed them with slightly more legible handwriting (Ochsenius, 1904: 149). Fortunately, a photocopy of the handwritten manuscript is now housed in the archives

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of the Deutsch-Chilenische Bund/Liga Chileno-Alemana (Santiago). Even more fortunately, Carlos Köbrich Uslar prepared a typewritten version in 1993, which although not having the same pagination as the handwritten original, is far more legible and has been quoted herein (the typewritten version is in the Liga Chileno-Alemana, with a photocopy in the Bibliothek des Naturkundemuseums im Ottoneum, Kassel, Germany). Gotschlich (1904) quoted from the autobiography, but as it remained in possession of Philippi's descendants, it was largely overlooked until recent years, when it was extensively used by Patience Schell, a historian of science, in her thorough analysis of Darwin, Philippi, and other naturalists in Chile in the 19th century (Schell, 2013); previously, two historians of science quoted from the handwritten version (Blancpain, 1974; Wunder, 1988), and the section covering the 1848 revolution in Germany and Philippi's move to Chile was translated into French (Blancpain, 1974: 1061–1065). Recently, most of this autobiography was translated into Spanish with extensive annotations (Philippi, 1897–1898).

Four of Philippi's colleagues authored lengthy contemporaneous memorials that provide additional information from a variety of perspectives, although bordering on hagiographies: Diego Barros Arana (1830–1907), the first historian of Chile and a faculty colleague of Philippi at the Universidad de Chile (Barros Arana, 1904); Paul Fürstenberg, an educator in Berlin and Chile (Fürstenberg, 1906); Bernhard (Bernardo) Gotschlich (1877–1931), Philippi's last research assistant at the Museo (Gotschlich, 1904); and Carl-Christian Ochsenius (1830–1906), a civil engineer and geologist who emigrated on the same boat with Philippi from Hamburg to Chile (Ochsenius, 1906). Several shorter appreciations of Philippi were published after his retirement and before his death (Amunátegui, 1896; Anonymous, 1898; Ochsenius, 1889). In the century subsequent to Philippi's death, both the Chileans and the Germans have published extensively on Philippi's life, with an emphasis on his exploration of Chile and his botanical contributions.

#### R. A. PHILIPPI'S EARLY YEARS

The origin of the Philippi family name is uncertain. Although there are records of individuals named "Philippi" in France in the 1600s–1700s,

the earliest known connection of this name with R. A. Philippi is his great-grandfather, Gerardus Philippi (also known as Gerdt Philip) (1665–1736), a life-long native of Hamm, then a small town in the Ruhr district, northwestern Germany. His son, Franciscus Wilhelmus Philippi (1710–1768), also a native of Hamm, had a son, Johann Wilhelm Eberhard Philippi (1761–1836), born in Hamm, and who moved to Berlin (Otto, 1961; Schwarzenberg de Schmalz, 1968: 65). J. W. E. Philippi, an auditor for the Prussian government, had five children from two previous marriages, and then married Maria Anna Krumwiede in 1806. Their son Rudolph Amandus Philippi was born on 14 September 1808, in Charlottenburg, which was then a western suburb of Berlin, and is now within its city limits. Philippi was the oldest of two children of this marriage; Bernhard Eunom Philippi (1811–1852) was his younger brother.

In 1818, at a relatively young age, Rudolph and Bernhard went with their mother to Yverdon, Switzerland, ostensibly so that the boys could be educated at the Pestalozzian Institute, set up by Johann Heinrich Pestalozzi (1746–1827). This elementary school was known for its innovative teaching methods, particularly the use of real objects to teach the natural sciences, at a time when most education was pure rote learning and memorization, and it had a significant effect on the Philippi brothers (Philippi, 1895). Philippi, late in his life, particularly recalled making collections of plants and butterflies while in Yverdon (Philippi, 1895: 144; 1904: 322). However, Blancpain (1974: 81–82) and Schell (2013: 113) revealed what Philippi had buried in his handwritten autobiography – the real reason that the brothers were sent to Switzerland with their mother was because their father had impregnated the family housekeeper, which broke up the marriage, leading to a separation.

Philippi, his mother, and his brother then returned to Berlin in 1822, where he [Rudolph] studied at the Königliche Gymnasium zum Grauen Kloster (founded in 1574 and closed by the East Germans in 1958), equivalent to a high school. In 1826, Philippi began his studies at the relatively new Friedrich-Wilhelms-Universität Berlin (founded in 1810 as the Universität zu Berlin and now known as the Humboldt-Universität zu Berlin), where he graduated in 1830 at the age of 21 (Ochsenius, 1906: 17–18). Although his degree was nominally in medicine and surgery, his coursework included botany, entomology, comparative



anatomy, several courses in vertebrate zoology, and, perhaps most importantly for Philippi's future work, "Physische Geographie" (which included biogeography), taught by Alexander von Humboldt (1769–1859), who had extensively explored the northern part of South America from 1799 to 1804; his publications on South America significantly inspired Charles Darwin and others who explored that continent.

Philippi's 1830 dissertation, surprisingly, was on the grasshoppers of Berlin (*Orthoptera Berolinensia*), but in those days, the professor usually assigned the thesis topic, and the student was not expected to devote the rest of his life to that field.

After graduating with highest honors (*summa cum laude*) in the spring of 1830, Philippi had the first of several respiratory diseases (probably influenza or pneumonia), so he went to Italy for the warmer weather. Philippi spent over a year and a half traveling around Italy, initially in the company of two geologists, Friedrich Hoffmann and Arnold Escher von der Lind, and they studied the volcanoes at Etna and Vesuvius. Here Philippi made the first of his large collections of fossil and Recent molluscs from Sicily (Philippi, 1898: 402; 1904: 322). Philippi was among the first of numerous German zoologists who travelled to Italy, particularly to Messina, Sicily, and to Naples, to study the then-exotic marine fauna in its natural setting (Groeben, 2008: 143, 149–150). Philippi (1902: 5) described how he spent time with Emiliano Guttadauro (1759–1836), an Italian Benedictine priest and shell collector with a sizable collection and library (Tornabene, 1839), which apparently motivated Philippi to focus on molluscs:

Er ... hatte eine recht hübsche Conchilien-sammlung und fast alle der teuren älteren Conchilienwerke, die früher der königlichen Bibliothek in Neapel angehört hatten, bei der Erstürmung des königlichen Palastes aber vom Pöbel geraubt und auf den Strassen feilgeboten waren, wo der Pater sie für ein Spottgeld gekaufte hatte.

[He ... had a quite beautiful shell collection and almost all of the expensive, rare shell books, which formerly belonged to the Royal Library in Naples. During the storming of the Royal Palace [in 1820?], these books were stolen by the mob and sold on the streets, where the Father was able to buy them for a ridiculously low price.] (Philippi, 1902: 5).

Philippi returned to Berlin in 1832 by way of Paris, in order to complete his examinations in

medicine in 1833, although he never practiced as a physician.

Philippi initially had difficulties finding employment in natural history, but in February 1835, he was hired as a teacher in natural history at the Höhere Gewerb-Schule (equivalent to a teacher's college) in Cassel, which was founded in 1832. Cassel (known as Kassel since 1926), a small university town in northern Germany, was long known for its natural history museum, the Ottoneum, which has its origins in the 1568 Naturalienkabinet, and is among the oldest such museums in Germany. One year later, he married his first cousin Caroline Krumwiede on 1 January 1836. Philippi, decades later, revealed one reason for marrying her: "Mon salaire était très modique, mais ayant épousé une cousine qui avait une petite fortune, je pouvais vivre et consacrer mon temps libre à l'étude des Testacées." [My salary was very modest, but having married a cousin who had a small fortune, I could survive and devote my free time to the study of shells.] (Philippi, 1904: 322). Also, Philippi was able to use some of the specimens he collected in Sicily to trade for molluscs from other, exotic localities (Philippi, 1904: 322). Meanwhile, Philippi started publishing several short articles on various natural history topics, and devoted his free time to studying the molluscs that he had collected in Sicily and the nearby regions of southern Italy.

In early 1836, Philippi published his first major malacological work, the *Enumeratio molluscorum Siciliae cum viventium tum in tellure Tertiaria fossilium quae in itinere suo observavit*, printed in Berlin. This analysis of the molluscs of Sicily (discussed more fully below), was presented by Alexander von Humboldt to Kaiser Friedrich Wilhelm III, then the ruler of Prussia, who awarded a gold medal ("Goldene Medaille für Kunst und Wissenschaft") to Philippi on 14 April 1836 for this book (Gotschlich, 1904: 16; Ochsenius, 1906: 19).

April 1836 was also significant in that Philippi was one of 15 founders of the Vereins für Naturkunde (Natural History Society), in Cassel, and was its first director (Schrader, 2004: 326). This natural history society was renamed in 1980 in his honor as the Philippi Gesellschaft zur Förderung der Naturwissenschaften, and it remains active today, although renamed yet again in 2005 as the Nordhessische Gesellschaft für Naturkunde und Naturwissenschaften (Moog, 1986; Nitsche, 2011: 18–25; Hedewig, 2005). The affiliated



Naturkundemuseum im Ottoneum publishes a journal, *Philippia* (1970–present), devoted to the natural history of the region around Kassel (Follmann, 1970).

Philippi, in July 1837, was again diagnosed with pneumonia and told by his physician that he only had a few years left to live, and that he should move to a drier climate in order to alleviate the symptoms (Philippi, 1897–1898: 144; 1902: 26–27; Ochsensus, 1906: 19). Thus, he returned to Sicily, where he spent several years exploring and collecting the fossil and Recent molluscs of Sicily, Naples, and adjacent regions. Philippi became well acquainted with Arcangelo Scacchi (1810–1893), an Italian malacologist, who introduced Philippi to a local collector whom Scacchi had trained to collect marine life, and to an old woman who provided Philippi with the seaweeds and mud that was brought up with the fishermen's nets, which Philippi found invaluable in having numerous small gastropods, bivalves and crustaceans (Philippi, 1897–1898: 163). Many of Philippi's detailed watercolor drawings of these organisms are now archived in the Liga Chileno-Alemana (Santiago). His third child, Friedrich Heinrich Eunom Philippi was born in Naples in 1838 (two earlier children had died as infants). Fortunately, Philippi was able to outlive his physicians, for he fully recovered; in 1903, he wrote to an Italian paleontologist that his time in Italy in the 1830s had completely restored his health (De Gregorio, 1908: 149). Philippi returned to Cassel in February 1840, by way of Switzerland, where he stopped in Neuchâtel to visit the paleontologist Louis Agassiz (Philippi, 1902: 49; Barros Arana, 1904: 38–39). In 1844, Philippi completed an enlarged and revised second edition of his book on the molluscs of Sicily (Philippi, 1844a). As before, Kaiser Friedrich Wilhelm IV, the new ruler of Prussia, awarded a second gold medal to Philippi for this book, just as his father had done in 1836 for the first volume. Philippi's research also led to Philippi becoming an honorary Knight in both the Kingdom of Italy (Cavaliere dell'Ordine della Corona d'Italia, 1868) and the Kingdom of Spain (Caballero de la Orden de la Isabel la Católica, 1866) (Gotschlich, 1904: 58–60; Ochsensus, 1906: 19).

Philippi's years in Cassel provided a remarkable opportunity for him to work with other malacologists and shell collectors, of whom there were few if any in Berlin in the early 1830s. In contrast, Cassel and its environs had a significant circle of malacologists, perhaps the

earliest such cluster in Germany (Jungbluth, 2011). Karl Menke, who lived in Pyrmont, north of Cassel, had founded the *Zeitschrift für Malakozoologie* in 1844 – the first “modern” German malacological serial. After two volumes, Louis Pfeiffer (1805–1877), a banker in Cassel with strong interests in both land snails and cacti, became a co-editor of the journal, which was then published in Cassel from 1846 through 1853 (Kabat & Coan, 2016). Another shell collector in Cassel, Friedrich Carl Ludwig Koch (1799–1852), who was also known as a paleontologist, a mining engineer (with the title of Bergrat, or Minister of Mining), and the operator of a glass factory, was to prove quite important to Philippi in 1851 (Jarck, 1996; Krippendorff, 2000, 2006). Wilhelm Dunker (1809–1885), a colleague who taught mineralogy at Cassel from 1839 to 1854, also published extensively on fossil and Recent molluscs.

From a malacological perspective, the 1840s were to be by far the most active decade for Philippi in terms of the numbers of publications and descriptions of new species. In addition to the 1844-second edition of the Sicily book, he also authored and edited several other malacological series, as discussed below.

Meanwhile, Philippi's brother Bernhard Eunom Philippi, instead of going to a university, joined the German merchant marine in 1830 on a round-the-world trip that included a stop in Chile. In 1832, on a second trip, Bernhard left the ship in Valparaíso, and spent several years collecting specimens in Peru and Chile for the natural history museums in Berlin and elsewhere in Germany; Bernhard was paid 1,000 Prussian Thalers for his collecting efforts (Philippi, 1897–1898: 245). Bernhard became so enamored of Chile, that he returned in 1841, with a grand plan to encourage German emigration to the southern part of that country. Chile had only recently become independent from the Viceroyalty of Peru, after the Chilean War of Independence, which lasted from 1810 to 1823, and was spearheaded by the half-Irish liberator of Chile, Bernardo O'Higgins. But, even after independence, the colonization by the Spanish-speaking immigrants was largely concentrated in Santiago and the central coastal region, and the national government's control over the southern regions was tenuous. Thus, the Chilean government ultimately agreed to Bernhard's proposal that Germans emigrants – preferably Catholics – would settle in Valdivia and adjacent regions. Bernhard was also instrumental in seizing control of



the Strait of Magellan for Chile in 1843, and building the first fort near what is now Punta Arenas. However, the Chilean government was soon unhappy with the fact that most of the Germans who wanted to immigrate to Chile were Protestants from northern Germany, not Catholics from Bavaria, so that Bernhard was given the thankless task of serving as the first governor of the barely settled Magellan Province, the southernmost in Chile (Blancpain, 1974: 81–89, 152–166; Konrad Mayer & Siebert Held, 2002: 42–52, 58–60; Philippi, 1903; Tampe Maldonado, 1977: 17–22; Wunder, 1988: 362–366).

Meanwhile, March 1848 was the start of the Revolution in Germany, which was part of several other wars and revolutions sweeping across Europe in that critical year. The 1848 Revolution, while ultimately leading to the unification of Germany as a single country, resulted in significant political and economic turmoil for several years. Although Cassel was not immediately affected by the civil war, Philippi and his malacological colleagues in Cassel soon found that they were unable to maintain the publication schedule of the *Zeitschrift*, as the monthly issues for 1848 and 1849 soon fell well behind schedule (Kabat & Coan, 2016). Philippi was promoted to director of the school in Cassel in 1848. By late 1850, the Revolution had reached Cassel, and Philippi found himself on the wrong side of the conflict in northern Hesse – he was considered to be a liberal and was threatened when some 25,000 military troops from Bavaria and Austria, on behalf of the conservative forces, invaded Hesse in November 1850. Philippi was able to escape Cassel in December 1850 with the assistance of Koch (whose daughter was engaged to Bernhard, although they never did marry); Koch warned Philippi of the need to leave, and provided him with a safe-house in Karlshütte (near Delligsen, Lower Saxony), where Philippi waited for an opportunity to leave the country (Krippendorff, 2006; Barros Arana, 1904: 49–57; Blancpain, 1974: 1061–1065; Ochsenius, 1906: 20; Philippi, 1897–1898: 237; 1898: 403; 1904: 323; Wunder, 1988: 367–369). Philippi formally resigned his government position as Rector on 27 December 1850 (Gotschlich, 1904: 26–27).

On 26 January 1851, Philippi wrote a heartfelt farewell message to the subscribers of his *Abbildungen und Beschreibungen* that he was leaving Germany because of the political events:

... indem ich durch die beispiellos in der Geschichte da stehenden Ereignisse, welche sich in den letzten Wochen in Kurhessen zugetragen haben, veranlasst worden bin, meine Stellung in Kassel aufzugeben, in welcher ich seit beinahe vollen sechszehn Jahren wirksam gewesen bin, in der ich aber in Zukunft wenig Freude mehr erwarten durfte. Ich ... hoffe fest, dass es mir gelingen wird, ein Plätzchen zu finden, wo man reden und handeln darf, wie es das Gewissen gebietet, und wo das Festhalten an geschworenen Eiden kein Verbrechen ist.

[The unprecedented ... events which have occurred in the recent weeks in Kurhessen forced me to give up my position in Kassel, in which I have been active for nearly a full sixteen years, in which I but could expect little more joy in the future. I ... firmly hope that I will succeed to find a place where you can speak and act as conscience requires, and where the adherence to sworn oaths is not a crime.] (Philippi, 1851: [i]).

Because Philippi's brother Bernhard had so extolled the virtues of Chile, Philippi decided to join him there, leaving his family (by then there were five living children, one of whom died in 1853) in Germany. Alexander von Humboldt wrote to Philippi on 11 March 1850, encouraging him to explore Chile, which Humboldt had not visited himself; Humboldt was particularly interested in the cold current, now known as the Humboldt Current, the wild potato, and the fossils of Chile (Schell, 2013: 120; translated into Spanish by Gotschlich, 1904: 28–29; Eyzaguirre Philippi, 2008b: ix; and Cubillos Osorio, 2002: 42). Humboldt also provided a "letter of introduction" for Philippi, which greatly praised his talent, and expressed great regret that Philippi was leaving Germany ("Er verließ Deutschland zu unserm Bedauern") (Schrader, 2004: 332; translated into Spanish by Cubillos Osorio, 2002: 41). Humboldt's two letters, translated into Spanish, are engraved on large stone tablets in front of the Museo Nacional de Historia Natural, Santiago (Schrader, 2004: 332).

On 20 July 1851, Philippi left Germany, never to return, on the *Bonito*, sailing from Hamburg to Chile. Philippi arrived in Valparaíso on 4 December 1851, after 135 days at sea, as the ship was significantly delayed due to storms at Cape Horn. Philippi used the time on the ship well – not only did he complete his *Handbuch der Conchyliologie und Malacologie* (published in Germany in 1853), but also he learned Span-



ish sufficiently well to be reasonably fluent upon arrival in Chile (Henze, 1995b: 99).

Philippi was not the only German naturalist to escape to Latin America as a result of the 1848 Revolution. Hermann Burmeister (1807–1892), who received his M.D. at Halle, where he taught zoology and specialized in entomology, also had to leave Germany in 1850, travelling first to Brazil (1850–1852) and then to Uruguay and Argentina (1856–1860), and permanently settled in Argentina in 1862, where he was the first director of what is now known as the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires) (Adler, 1989: 45). As Sanhueza Cerda (2006: 55) noted, “La biografía de Burmeister es similar a la de Philippi: estudios parecidos; semejantes dificultades y una destacada labor científica y académica en el país anfitrión.” [Burmeister’s biography is similar to that of Philippi: similar studies; similar difficulties and outstanding scientific and academic work in the host country.]. Similarly, Fritz Mülller (1821–1897), the entomologist best known for discovering Mullerian mimicry of insects, also left Germany for Brazil in 1852 because of the aftermath of the Revolution. Philippi, Burmeister, and Müller were among the more than 50 German naturalists who explored South America in the 1800s, many of whom were sent or inspired by Humboldt (Hoppe, 2001: 215–218).

Unfortunately, less than one year after Philippi’s arrival, his brother Bernhard was killed by the natives near Punta Arenas in late October 1852 (Schell, 2013: 123), and his nephew Theodor, who became a botanist and a schoolteacher in Concepcion, died from an ulcer in 1852. Philippi’s wife died in 1867 of dysentery (Schell, 2013: 168). Of Philippi’s four children who came to Chile with his wife in 1856, two died early: Mathilde (1842–1863) and Karl Eduard (1846–1870, killed in the Siege of Metz during the Franco-Prussian War, having returned to Germany for college).

## NATURAL HISTORY IN THE NEW WORLD

Although Philippi was the most significant and prolific naturalist in Chile in the 1800s, he was hardly the first to collect specimens and publish on the interesting flora and fauna of that country. The first major natural history collector in Chile was Juan Ignacio Molina (1740–1829), who was born in Talca in central Chile, educated in Concepcion, and became a Jesuit priest.

However, the Jesuits were expelled from Chile and other Spanish colonies in 1768, so Molina escaped to Bologna, Italy, where he spent the rest of his life, describing the Chilean flora and fauna without having further access to Chile (Jaksic et al. 2012: 40–53; Medel, 2008: 319; Ronan, 2002; Guerra, 1974: 458). The *Saggio sulla Storia Naturale de Chile* (Molina, 1782) included descriptions of about 20 new species of marine invertebrates from Chile, including the ecologically important mussels *Aulacomya ater* (Molina, 1782) and *Choromytilus chorus* (Molina, 1782), and a number of decapod crustaceans (Jara, 1997: 248–249). In 1867, Philippi prepared a detailed commentary on the animals described by Molina; Philippi’s harsh criticism of Molina “shows little sympathy for the handicaps under which Molina worked and exhibits a definite bias against him” (Ronan, 2002: 192).

In 1822, Hugh Cuming (1791–1865), an English sailmaker, arrived in Valparaiso, and spent the next several years collecting marine shells in Chile. From October 1827 to June 1828, he collected extensively in what is now French Polynesia, returning to Valparaiso. Cuming made a lengthy expedition along the Pacific coast of South and Central America, from Valdivia to Honduras, again returning to Valparaiso, and he ultimately returned to England in 1831 (Coan, 2011; Dance, 1986: 110–115). W. J. Broderip and G. B. Sowerby I described numerous new species from the specimens Cuming collected in Chile (Dance, 1986: 116). In the 1840s, Philippi described some new species from Cuming’s specimens, mostly in the Littorinidae and Naticidae.

The first German naturalist to explore Chile was the botanist Eduard Friedrich Poeppig (1798–1868), who studied in Leipzig, and is best known for his travels across South America from 1827 through 1832, resulting in the two-volume *Reise in Chile, Peru und auf dem Amazonenstrome während der Jahre 1827 bis 1832* (1835–1836) (Löschner, 1978: 117–118; Zirstein, 2000b: 572–573). Poeppig was significantly influenced by Alexander von Humboldt, whose travels in Peru and elsewhere in the northern part of South America from 1799 to 1804 led to major insights on plant biogeography (Sanhueza Cerda, 2010). Although Poeppig mostly collected and described plants, he also described several species of decapod crustaceans from Chile.

The first European naturalist to spend extensive time in Chile was the French botanist Claude [Claudio] Gay (1800–1873), who





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FIG. 1. R. A. Philippi, circa 1840 (reprinted from Jaksic et al., 2012: 74, original in Seccion Botánica, Museo Nacional de Historia Natural, Santiago).  
FIG. 2. R. A. Philippi, sculpture, Museo Nacional de Historia Natural, Santiago (circa 1870s?).  
FIG. 3. Chile, postage stamp of Bernardo and R. A. Philippi (1978, first day cover).  
FIG. 4. R. A. Philippi, painting (circa 1880s?) (reprinted from Fundacion R. A. Philippi de Estudios Naturales, Chile).



studied botany in Paris, and then emigrated to Valparaíso, Chile in 1828 (Schell, 2013: 34–57), where he became the first natural sciences teacher in Chile, at the Colegio de Santiago (equivalent to a high school). In 1830, the Chilean government arranged for Gay to spend the next three years exploring Chile, not just its natural history, but also its economic resources (Jaksic et al., 2012: 62–73; Donoso Saint & Sagredo Baeza, 2012: 15–40, 247–254; Schell, 2013: 41). In 1842, Gay returned to Paris for the rest of his life, with his extensive collections, and published the *Historia física y política de Chile* (1844–1871), which appeared in 28 volumes, with a two-volume atlas. Gay was the author of the eight-volume “Historia,” the two-volume “Documentos,” most of the eight-volume “Botánica,” the two-volume “Agricultura” and the Mammalia section of the eight-volume “Zoología.” The molluscs, including fossils, were described by Louis Hippolyte Hupé (1819–1867) in the eighth volume of the Zoología series (Hupé in Gay, 1854; Griffin & Nielsen, 2008).

Unfortunately, Gay’s careless approach towards recording the exact locality of the specimens that he collected severely limited the accuracy or utility of the species descriptions (Schell, 2013: 111, 150–153). Jara (1997: 249) noted, “Además se constata, según los críticos, una falta de precisión en la referencia a las localidades de recolección del material, i.e., ‘Chile’, ‘costas de Chile’, etc.” [Critics also note the inaccurate or imprecise localities for the specimens, such as “Chile” or the “coast of Chile”]. Also, since Gay took his entire collection to Paris, where they remain today, this meant that when Philippi arrived in Santiago, the national museum had almost nothing in its collections, as Philippi (1887a: 1; 1887b: 1) was later to complain:

Als ich im Jahre 1853 die Direction des Museums von Santiago übernahm, fand ich in demselben kaum ein Dutzend chilenischer Versteinerungen vor, sei es aus der Jura-, sei es aus Jüngern Formationen. Herr Gay, der frühere Director, hatte alle die von ihm in Chile gefundenen nach Frankreich genommen, und sind dieselben von Herrn Hupe in Gay’s *Historia física i política de Chile* (Zoología, Bd. 8) beschrieben; nur das eine oder andere Exemplar war zufällig im Museum liegen geblieben.

[When I became director of the Museo in Santiago in 1853, I found barely a dozen Chilean fossils, whether from the Jurassic or

from younger formations. Mr. Gay, the former director, had taken all the fossils collected by him in Chile to France, including those described by Mr. Hupé ... only a few specimens were left at random in the Museo].

Philippi (1898: 404) later described the Museo as of 1853 as a “Rumpelkammer” (junk room), filled with random objects.

The next significant naturalist to visit Chile was Alcide d’Orbigny (1802–1857), who collected numerous fossil and Recent molluscs from Argentina, Chile and Peru during his 1826–1833 travels in South America. These were described in the *Voyage dans l’Amérique Méridionale* (d’Orbigny, 1842–1843); the Cenozoic fossils from Chile and Argentina have been analyzed (Griffin & Nielsen, 2008).

The most famous naturalist to visit Chile in the 1800s was, of course, Charles Darwin (1809–1882), who spent over two years exploring Argentina and Chile from 1833 to 1835, far longer than he spent in the Galapagos, and his observations in Chile greatly influenced his paleontological thinking (Allmon & Smith, 2009). The fossil molluscs collected by Darwin were described by George B. Sowerby II (1812–1884), as part of Darwin’s *Geological Observations on South America* (G. B. Sowerby II, 1846; Griffin & Nielsen, 2008). Darwin, while in Valparaíso in 1834, wrote to his mentor, the botanist John Stevens Henslow, perhaps half-facetiously, that “I had hoped during this time to have made a good collection of insects but it has been impossible. I regret the less, because Chili fairly swarms with Collectors; there are more Naturalists in the country, than Carpenters or Shoemaker[s] or any other honest trade.” (Burkhardt & Smith, 1985: 401). Philippi was later to take advantage of this network of naturalists in Chile.

Also arriving in Chile in the 1830s was Ignacio Domeyko (1802–1889), a Lithuanian Pole, initially exiled from Poland to Paris in 1830, where he studied geology, particularly mineralogy, and then emigrated to Chile in 1838 (Grigelis, 2005: 279–280; Donoso Saint & Sagredo Baeza, 2012: 41–65, 254–261; Schell, 2013: 94–95). Domeyko soon met Gay, and later became a long-time faculty colleague of Philippi. Domeyko eventually became the Rector (president) of the Universidad de Chile, and was noted for his collections of fossil vertebrates of Chile, particularly from Patagonia. Domeyko was quite formal in his relationships with the students, who viewed him as reactionary at a time when the students



were clamoring for greater academic freedom (Schell, 2013: 171); in contrast, the students were much fonder of Philippi. Domeyko's lengthy autobiography made no mention of Gay (Schell, 2013: 102), and briefly mentioned Philippi in only one sentence regarding his Atacama travels (Domeyko, 1963: 234; 1978: 444); in contrast, Domeyko devoted three sentences to a chance encounter with Bernardo Philippi in Valdivia in 1845, where they found a luminescent toad (Domeyko, 1963: 501; 1978: 721–722), although Domeyko went on to criticize Bernardo's work in bringing Protestants, not Catholics, to southern Chile (Schell, 2013: 209).

### PHILIPPI'S LIFE IN CHILE

Philippi became the director of the Lyceum (high school) in Valdivia in 1853. Philippi had arrived in Chile at a time of political turmoil and suppressed revolutions in the south, but was able to avoid political controversies (Ochsenius, 1999: 35–36). In October 1853, Manuel Montt, the President of Chile, appointed Philippi to be the Professor of Zoology and Botany at the Universidad de Chile (Santiago), and that same month also appointed him to serve as Director of the Museo de Historia Natural, which was then located at the university (Gotschlich, 1904: 34–36). Philippi initially taught both zoology and botany, and later added courses in natural history and physical geography (Barros Arana, 1904: 104, 157).

In November 1853, only one month after these appointments, the Chilean government took advantage of Philippi's geological skills, and made him the director of an expedition to explore the vast Atacama Desert, which was then spread across three countries: Chile, Peru and Bolivia. Although Philippi collected some molluscs and other natural history specimens in the world's highest and driest desert, the significance of his explorations were his geological observations, including the extensive nitrate or saltpeter deposits (then an important ingredient for fertilizer and explosives), as well as realizing that the region contained economically valuable copper resources (Donoso Saint & Sagredo Baeza, 2012: 67–91, 261–268; Kurtz, 1979; Muñoz Schick, 2008; Nuño García & Niño Valenzuela, 2003; Schell, 2001, 2013: 139–144; Scuria, 1982: 255–259; Soto Nardecchia, 2008: 16; Steffen, 1910a: 202–203, 1910b: 196–197). In contrast to Darwin, who

visited the Atacama during its normal drought stage, Philippi saw it shortly after a rare rainy period, when it was filled with small flowers and insects that fed on the flowers (Francaviglia, 2016: 125).

Philippi returned to Santiago in April 1854, and took several years to write up the results of his collections, which was published in separate German and Spanish volumes in 1860, as the *Reise durch die Wüste Atacama: Auf Befehl der Chilenischen Regierung im Sommer 1853–54 unternommen und beschrieben / Viage al desierto de Atacama hecho de orden del gobierno de Chile en el verano 1853–1854*. This book included 27 plates, of which two had fossils, seven had animals (mostly vertebrates), six had plants, and the remaining twelve had scenes of the small towns and mountainscapes of that region (reprinted in Philippi Izquierdo, 1973); the plates were reproduced from Philippi's original drawings made during his travels. Philippi also published several shorter notes, including the first description of the giant meteor crater in the Atacama, which led to his being praised by James M. Gillis, the Superintendent of the U.S. Naval Astronomical Expedition: "The recognized ability of the author – Dr. R. A. Philippi – is a sufficient guaranty for the accuracy with which he will make known every incident of his journey to that inhospitable region" (Gillis, 1855: iv). The Chilean government eventually realized the strategic importance of this region, for in 1879, Chile declared war on both Bolivia and Peru (after Bolivia had declared war on Chile), and the result was a major victory for Chile, which captured the entire coastal region of Bolivia (leaving it a landlocked country) as well as the southernmost provinces of Peru, resulting in almost the entire Atacama region and its mineral resources becoming located within Chile (Brintrup, 2011; Schell, 2001; Talbott, 1974: 33–50).

After the Atacama expedition, Philippi continued his practice of making detailed and realistic drawings of the Chilean landscape, most of which remained unpublished until his great-grandson published them with annotations (Philippi Izquierdo, 1973). However, some of those drawings were not original to Philippi, but were copied from drawings made by Alexander Simon (1805–1852), a German artist who spent the last few years of his life in Chile with Bernhard Philippi before dying in unknown circumstances in Patagonia (Pereira Salas, 1968; Löschner, 1978: 119; Krauss,



2005: 25–28). While some of the original drawings of Philippi kept in the Archivo Emilio Held Winkler (Santiago) indicate in the border that they were copies of those by Simon, this attribution has been largely disregarded in later reprints of the works (J. M. Izquierdo König, pers. comm., 1 Apr. 2016).

### PHILIPPI AND THE OUTSIDE WORLD

Although Philippi never left South America – unlike Domeyko who returned to Poland for a hero's visit in 1884, only to come back to Chile to die (Schell, 2013: 207–208) – Philippi was hardly isolated from the broader scientific community. In addition to continuing to publish in German serials, and founding the *Anales del Museo Nacional* as a publication venue for the museum research (now titled the *Boletín del Museo Nacional de Historia Natural*), Philippi was an important figure for overseas scientists visiting Chile. When the *Comisión Científica del Pacífico*, the 1862–1866 Spanish scientific expedition that collected over 82,000 specimens in South America, landed at Valparaíso in 1863, the naturalists made their way inland to Santiago. Philippi introduced them to a number of other naturalists and collectors, and the naturalists admired Philippi's exhibits in the museum and the museum's fine library (Calatayud Arinero, 1994: 115–116; Miller, 1968: 73–74).

The Swiss naturalist Johann Jakob von Tschudi (1818–1889), who spent much of his life exploring South America, reached Santiago in 1859 and visited Philippi at the (old) Museo in Santiago (Tschudi, 1869: 145–147). Tschudi particularly praised Philippi for his curatorial work: “ich sage, dass es die bedeutendste und best-geordnete naturhistorische Sammlung Südamerikas ist ...” [I say that this is the most important and best-ordered natural history collection in South America], compared with the other institutions he had visited in Brasil, Montevideo and Buenos Aires (Tschudi, 1869: 145–146). Tschudi, in his travels across Chile, particularly noted the gigantic Atacama cactus and the endemic Andean flamingo, both described by Philippi (Tschudi, 1869: 48, 53–54). However, Tschudi also tartly noted the errors made by Philippi in calculating distances across the uncharted Atacama (Tschudi, 1869: 55).

Louis Agassiz, in 1872, near the end of his career at Harvard and barely one year before his death, went on the *Hassler Expedition* to South

America, ostensibly to test Darwin's theories, to no avail. However, the other naturalists on this expedition collected huge series of specimens, and Agassiz enjoyed his reunion in May 1872 with Philippi in Santiago – some three decades after Philippi met him in Neuchâtel (Hill, 1872: 8; Irmscher, 2013: 328). Domeyko, however, overshadowed Philippi by giving Agassiz “duplicates of his entire collection of [vertebrate] fossils, by far the most complete and valuable in South America, and which he has been thirty-five years in collecting, so that the museum of Professor Agassiz [the MCZ] will have the most complete collection of South American fossils ever made” (White, 1872: 3).

### PHILIPPI'S LATER YEARS IN CHILE

Philippi's family – his wife and four children (they had a total of ten children, but six died young) – arrived in Chile in December 1856, after a separation of nearly six years (Philippi, 1897–1898: 194). His family lived on Philippi's farm near Valdivia where Philippi spent his summers while on vacation from teaching in Santiago. Unfortunately, in November 1863, a fire destroyed his Valdivia residence, resulting in the loss of part of his personal archive of his research notes and manuscripts, including some notes from his years in Sicily (Philippi Izquierdo, 1973: 95). In 2007, a fire at the Universidad Austral de Chile, Valdivia, destroyed some of his zoological and botanical specimens and publications, along with copies of Darwin's and Humboldt's publications (Delmastro Naso, 2007; De Urresti Longton, 2007; Neira et al., 2007).

Philippi, after the publication of the Atacama book in 1860, was to spend most of the next several decades focusing on the plants, insects and vertebrates of Chile. He described relatively few Recent molluscs from Chile, and it was not until the 1880s that he was to publish extensively on the fossil molluscs of Chile.

In 1858, Philippi wrote to Guillermo Frick (1818–1905), a German friend in Valdivia, to recount a humorous comment that someone else had made about Philippi's dedication to natural history:

What is it that Philippi does? He hunts flies, and then he observes them through a large lens, and captures them in a drawing. It's surprising the way in which some men can earn their bread. [Translated from German into English by Schell (2013: 131–132); Spanish



translations by Eyzaguirre Philippi (2008a: 57, 2008b: viii) and Steenbuck (2003: 26)]. Philippi also taught in the natural sciences at the Universidad de Chile, and his textbook, the *Elementos de historia natural*, went through several editions (Johow, 1910a: 268–269, 1910b: 253–254; Camacho, 1971: 67–74). There has been extensive debate as to whether or not Philippi believed in Darwin's theory of evolution by natural selection. The consensus is that while Philippi in the 1860s did not initially believe in natural selection, he did briefly mention Darwin's concepts in the *Elementos*, for which he was to be harshly criticized (Jakšić et al. 2012: 82; Márquez Breton, 1982: 20–28; Wunder, 1988: 371). A contemporary remarked that:

Apénas publicado su libro, se desató contra él en la prensa conservadora i relijiosa una guerra implacable de dicterios i de ultrajes, por haber sostenido, se decia, i por enseñar, que el hombre provenia del mono.

[Immediately after his book was published, the conservative and religious press unleashed a relentless war of insults and outrage for having sustained, it was said, that man came from apes.]

(Barros Arana, 1904: 146). The irony was that Philippi, in the 1860s and later, did not fully believe in Darwinism (Schell, 2013: 177–179), yet was attacked for his book:

De hecho, es una ironía de la historia que el naturalista Philippi ... hubiera sido duramente atacado y denostado por la prensa religiosa y conservadora de la época. Fue la primera manifestación pública en contra de las ideas de Darwin en el país.

[It is a historical irony that the naturalist Philippi ... was harshly attacked and vilified by the religious and conservative press of the time.

It was the first public demonstration against the ideas of Darwin in this country.]

(Medel & Veloso, 2009: 15). Sometime around 1880, Philippi wrote, in Spanish, a one-page manuscript essay, "El studio de las ciencias naturales," which has been widely reprinted (Philippi Izquierdo, 1973: 13–14; Larroucau, 2003: 94; Schrader, 2004: 331; translated into German by Schrader, 2004: 330, and partial translation into English by Schell, 2013: 170). That essay attempted to reconcile natural history and religion, by arguing that there was "nothing more sublime, nothing more religious than the study of nature" ["Nada mas sublime, nada mas relijioso que el studio de las naturaleza"], and that understanding nature would

"form a more perfect idea of the Supreme Author" ["se formará sin duda un idea mas perfecta del Autor Supremo"].

Even in 1887, Philippi still was non-committal as to whether the changes that he observed in the composition of Chile's fossil molluscan fauna, from one geological period to the next, reflected evolution or cataclysms (creationism):

Haben wir in Chile Beweise, dass eine Art sich allmählich in eine andere verwandelt hat, wie die Darwinisten annehmen? Dies sind wichtige Fragen, über welche ein sorgfältiges und gewissenhaftes Studium der fossilen Ueberreste der Quartärzeit im Vergleich zur heutigen Meeresfauna einiges Licht werfen dürfte. (Philippi, 1887a: 252–253).

Tenemos pruebas de que una especie se haya trasformada en otra, como pretenden los darwinistas? Estas son cuestiones graves, sobre las cuales en studio prolijo i concienzudo de los fósiles de los depósitos cuaternarios i de la fauna marina actual podrán dar alguna luz. (Philippi, 1887b: 243).

[Do we have in Chile evidence that one species has gradually transformed into another, as claimed by the Darwinists? These are important questions, for which a careful and conscientious study of the Quaternary fossils compared to the Recent marine fauna is likely to shed some light.]

Philippi's 1899 book on the Jurassic fossils of Chile made no mention of these issues, probably because it was only the first of three intended volumes and did not contain a synthesis.

In 1875, Benjamin Vicuña Mackenna, the highly influential, half-Irish mayor of Santiago who significantly modernized the city, had organized a major international exposition in Santiago, which resulted in the building of a gigantic exposition hall in a park on the outskirts of Santiago. After the exposition, Mackenna and others convinced the Chilean government to convert the hall into what is now the Museo Nacional de Historia Natural (Schell, 2013: 181–182). Although Philippi was initially reluctant to move his collections and the library so far from the rest of the Universidad de Chile, he soon realized that the space was necessary to house these collections that had long ago outgrown the space at the Universidad. It helped that the government built a house on the park grounds, where Philippi was able to live with his research assistants and his son Friedrich (Federico), a botanist, and who ultimately suc-



ceeded Philippi as the Director of the Museo in 1897 (Fürstenberg, 1906: 241). Philippi devoted considerable effort to designing the exhibits and expanding the research collections; somewhat incongruously for a natural history museum, this one initially included “reliquias de la Guerra de independencia y de sus heroes y de la Guerra del Pacifico” [relics of the 1810–1823 War of Independence and the 1879 War of the Pacific] (Cárdenas Guedinot, 2003: 89).

In addition to his significant contributions to natural history, Philippi also was important in establishing other scholarly fields in Chile. In 1885, he was the founder and the first president of the *Deutscher Wissenschaftlicher Verein zu Santiago* (the German Scientific Society), which published the *Verhandlungen* from 1885 through 1913, with a new series from 1931 to 1936 (Krebs Kaulen et al., 2001: 122–125). In 1878, he was a founder and the first president of the *Sociedad Arqueológica de Santiago* (Archaeological Society of Santiago), a predecessor to the *Sociedad Chilena de Arqueología* (Gänger, 2014: 209–210).

In 1878, Wilhelm I, the first Emperor of Germany, awarded Philippi the “Königlicher Kronen-Orden dritter Klasse” (Order of the Crown, third class) for his 70th birthday (Gotschlich, 1904: 60–61). Twenty years later, in 1898, his grandson, Wilhelm II, the last Emperor of Germany, awarded Philippi the “Königlicher Kronen-Orden zweiter Klasse” (Order of the Crown, second class) for his 90th birthday (Gotschlich, 1904: 62–63).

On Philippi’s 80th birthday in September 1888, the German community in Santiago and Valparaíso had a three-day celebration in his honor, particularly for his role in teaching so many prominent Chileans (Anonymous, 1888).

In 1890, the University in Berlin awarded Philippi an honorary doctorate degree, on the sixtieth anniversary of his 1830 thesis (Gotschlich, 1904: 50–52). Ten years later, Berlin awarded Philippi a second honorary degree, on the seventieth anniversary of his thesis (Gotschlich, 1904: 76–77).

For Philippi’s 90th birthday in September 1898, the Universidad de Chile had a “Homenaje” in his honor, which started out with a military band playing Wagner’s *Tannhäuser* march, followed by several speeches in his honor, including a poem of 137 lines (“A don Rodolfo A. Philippi en el Nonajésimo Aniversario de su Natalicio”), with elegiac lines such

as “¡Oh grande, oh inmortal Naturaleza tú fuiste su pasión!” [Great, immortal nature was your passion!], and closing with another Wagnerian piece performed by the military band (Anonymous, 1898; Schell, 2013: 224). Philippi received a gold medal with his image, the years 1808–1898, and the inscription “Al Doctor R. A. Philippi – sus amigos Chile” (Philippi Izquierdo, 1973: 12). Philippi responded with a heartfelt speech, in which he thanked Chile for being so receptive to foreigners, and stated that:

Una suerte benigna me ha permitido continuar estudiando la naturaleza, la única pasión que he tenido en mi vida i desde mi niñez, i me ha permitido también prestar algunos servicios a la ciencia i a mi querida segunda patria.

[Good fortune allowed me to continue in the study of nature, the only passion that I had in my life since childhood, and has also allowed me to provide some service to science and to my beloved second fatherland.] (Barros Arana, 1904: 195; Schell, 2013: 224); also translated into German by Fürstenberg (1906: 242).

In 1901, the 50th anniversary of Philippi’s escape from Germany to Chile, Philippi wrote several autobiographical essays (Philippi, 1901a, 1902, 1903, 1904). Antonio De Gregorio, an Italian paleontologist, wrote an encomium that rightly praised Philippi for his Sicily books as having laid the foundation for all future work on the Mediterranean molluscan fauna (De Gregorio, 1902).

In early July 1904, Philippi completed his last manuscript (unpublished, on Chilean frogs), and was diagnosed with pneumonia on 23 July 1904, which led to his death that day. The next day, his body was laid in state in the grand hall of the Universidad, where it was viewed by over 10,000 persons. The second day after his death was declared a school holiday in Santiago, and some 30,000 persons, including every schoolchild in Santiago, lined the 2.5 kilometer route from downtown to the Cementerio General. The horse-drawn funeral cortege, accompanied by 284 horse-drawn carriages containing the entire Chilean parliament and cabinet, along with numerous other government ministers, carried his body to its final resting place (Barros Arana, 1904: 204–211; Ochsenius, 1906: 55; Losch, 1905: 157 [15]). Gotschlich (1904: 120–156) devoted some 25 nearly overwrought pages to a detailed description of the memorial and funeral, down to the level of identifying and illustrating



the 40 different floral memorials, and with three photographs of the funeral procession.

It is safe to say that no other zoologist or paleontologist had such a large turnout at his funeral, although Alexander von Humboldt supposedly had “tens of thousands” of mourners at his 1859 funeral (Wulf, 2015: 280). Alas, as the cemetery in Santiago was then owned and operated by the Catholic Church, there was one final indignity, as Philippi was a German Lutheran up to his death. The Church required that all non-Catholics be buried in the separate “Patio de Disidentes” in the southwest corner of the Cementerio, which was sealed off from the rest of the cemetery by a wall that is about one meter thick and four meters high. Philippi’s family mausoleum, which has only been used by a few of his relatives, remains an imposing fortress (illustrated by Gotschlich, 1904: 156). The “Patio de Disidentes” is the final resting point for numerous other German Lutherans and several German Jews, along with merchants (Church of England), and ship captains (Church of Scotland) (A. Kabat, pers. obs.).

1904 was a noteworthy year in malacology, as three other German malacologists also died in that year: David Fr. Heynemann (born 1829), Franz M. Hilgendorf (born 1839) and Karl Eduard von Martens (born 1831), along with the French conchologists Arnould Locard (born 1841) and Jules Mabile (born 1831), and the English conchologist Frederick P. Marrat (born 1820).

#### PHILIPPI’S MALACOLOGICAL PUBLICATIONS

Philippi authored numerous malacological publications from 1834 to 1899, but the vast majority of his new taxa were described in eight monographs or series: (1) the 1836 and 1844 books on the molluscs of Sicily; (2) the 1841/1844 publications on the Oligocene molluscs of northern Germany; (3) the *Abbildungen und Beschreibungen* (1842–1851); (4) the treatments of a number of marine gastropod genera in Küster’s *Conchylien-Cabinet* (1842–1855); (5) the descriptions of 483 species in the “Centuria” articles in the *Zeitschrift für Malakozoologie* (1847–1852); (6) the *Handbuch der Conchyliologie und Malacologie* (1853); (7) *Die Tertiären und Quartären Versteinerungen Chiles / Los fósiles Terciarios i Cuatarios de Chile* (1887); and (8) *Los fósiles Secundarios de Chile* (1899).

Philippi’s first significant malacological work was on the Recent and fossil molluscs of Sicily, the *Enumeratio molluscorum Siciliae cum viventium tum in tellure Tertiaria fossilium quae in itinere suo observavit*, published in Berlin in 1836, with a second, expanded edition in 1844. Philippi described 347 species in these two books, which were written entirely in Latin, with full descriptions and synonymies, and he prepared the detailed illustrations himself. The dating of both editions has engendered some confusion in the literature. The 1836 book has a preface that is dated September 1835 and a title page dated 1836, but no indication of precisely when in 1836 it was published. However, since Kaiser Wilhelm III awarded Philippi the gold medal for this book on 14 April 1836, it must have been published sometime between January and April of 1836, and the publication date is here taken to be April 1836. Thus, the species described in Philippi’s book take precedence over those described by the Italian conchologist Arcangelo Scacchi later in 1836.

The second, revised and enlarged edition of the Sicily book similarly has a preface dated August 1843 and the title page is dated 1844, but no indication of precisely when in 1844 it was published. However, Philippi authored an “errata” in the July 1844 issue of the *Zeitschrift für Malakozoologie* (Philippi, 1844n: 100), in which he stated that “Kaum sind vier Monate verstrichen, seit dem der zweite Band meiner *Enumeratio Molluscorum Siciliae* die Presse verlassen hat” [barely four months have passed since the second volume of my Sicily book was published], which allowed Cretella et al. (2005: 115) and Janssen & Krylova (2012: 91) to determine that this book had to have been published in either January or February 1844 (Philippi, 1844a), thereby giving it precedence over a paper by Forbes (1844) on the molluscs from the Aegean Sea. Cretella et al. (2005: 115) stated that this errata “was most probably written in June at the latest, which means that the 2<sup>nd</sup> volume must have been published either in January or February 1844. ... the day being unknown, under the Code (ICZN, 1999: Art. 21.3) the publication date to be adopted is the last day of the month, that is, 29th February (1844 was a leap year).”

Philippi’s Sicily books are of significance in being among the first to provide comprehensive discussions of the Recent and fossil molluscs of the Mediterranean during the Pliocene and Pleistocene, although he and his successors



were scarcely aware of the complex paleontological history of that fauna. It was not fully appreciated until well over a century later, starting in the 1970s, that the Mediterranean Sea had dried up more than once during the Miocene, followed by alternating cycles in the Pliocene and Pleistocene of invasions of tropical species from western equatorial Africa and invasions of boreal, cold-water species from northern Europe, leading to a complex assemblage of molluscan taxa in the fossil record (Garilli, 2011: 100–102).

Philippi's Sicily books are also noteworthy in their detailed figures of living animals, done by Philippi himself; oddly, Philippi did relatively few such illustrations of molluscs in his later years. For example, the 1836 book has the first published illustrations of the gross anatomy of the enigmatic sponge-dwelling gastropod, *Siliquaria anguina* (actually a misidentified *Anguinaria obtusa*), although some details of the reproductive tract were misplaced (Bieler, 2004: 322). Carlo Gemmellaro, a well-respected geologist and paleontologist in Sicily, reviewed Philippi's 1836 book. Gemmellaro (1838: 103–104) noted that earlier efforts by foreigners to describe the Sicilian fauna were based on short trips and superficial analysis, but Philippi devoted far more time and effort to understand the fauna. Thus, Philippi's plates were "unquestionably accurate, colorful, and naturally drawn" so that this book was "the first and most complete ever published on the molluscs of Sicily" ["con indicibile accuratezza, e colorite al naturale in modo ... che essa è la prima e la più completa che si fosse fin'ora pubblicata sulle conchiglie di Sicilia"] (Gemmellaro, 1838: 108).

The second set of publications was on the fossils of northern Germany, which resulted in a preliminary, often overlooked publication in 1841, *Ueber die Tertiärversteinerungen der Wilhelmshöhe bei Kassel* (Philippi, 1841), which was then reprinted and significantly expanded in 1844, *Beiträge zur Kenntniss der Tertiärversteinerungen des nordwestlichen Deutschlands* (Philippi, 1844b). Subsequent authors did not always realize that the species in the first 32 pages of the 1844 publication were actually first described in the 1841 publication, or that the 1841 publication had the description of the new genus *Cerycium* (Strombidae), which was replaced in the 1844 edition with *Chenopus*. Although the book is dated "1843" on the title page, with a preface dated 5 March 1843, it was not actually printed

until the end of 1844, due to Philippi's delays in preparing the plates (Bronn, 1845: 510; Janssen & Kadolsky, 2016). Philippi described a total of 146 fossil molluscs from Germany, most in these two publications and in two other papers on the fossils of the region near Magdeburg, west of Berlin. These new taxa are mostly from the Oligocene, when Germany had a warm to tropical marine fauna, and include a number of key index species that remain of stratigraphic importance, including species of *Scalaspira* (Buccinidae) and *Streptochetus* (Fascioliidae).

Philippi, upon becoming established in Cassel, edited or contributed to three malacological publication series. Unfortunately, these became needlessly complicated in terms of determining the publication dates and priority, given their overlapping nature, and combined with the turmoil of the 1848 Revolution.

First, in 1842, Philippi founded the *Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien unter Mithülfe mehrerer deutscher Conchyliologen* [Illustrations and descriptions of new or poorly known shells, with the assistance of several German conchologists] (Philippi, 1897–1898: 200). This series was published in three volumes over a decade, ending in 1851, with each volume having 8 parts and 48 plates, for a total of 24 parts and 144 plates. This publication has numerous new taxa, most by Philippi, and others by his colleagues – identified on the title page of volume 1 as including Hermann Eduard Anton (1794–1872), Gerhard von dem Busch (1791–1868), Wilhelm Dunker (1809–1885), Israel Heymann Jonas (1795–1851), Friedrich Carl Ludwig Koch (1799–1852), Louis Carl Georg Pfeiffer (1805–1877), and Franz Hermann Troschel (1810–1882). Several other malacologists also contributed embedded descriptions of new species in Philippi's papers, including Christian Ferdinand Friedrich von Krauss (1812–1890), Johann Karl Megerle von Mühlfeld (1765–1840), Karl Theodor Menke (1791–1861), and Ludwig Parreyss (1799–1861).

However, the *Abbildungen* is needlessly complicated, because while several genera were treated in a single part, most of the genera were treated in multiple parts, sometimes divided among two or even all three volumes. In a misguided attempt to provide continuity, each page has dual pagination: the page number on the right-hand side is the page number for the volume as a whole, and the other page num-



ber on the left-hand side is for the genus as a whole. In the third volume, this page numbering scheme became even more complicated, with parts 1–4 having one set of numbers, and the numbering starting anew at “page 1” for part 5. Presumably the idea was that subscribers could either bind the parts as they were issued (the first set of page numbers), or could rearrange the parts in a taxonomic sequence (the second set of page numbers). Most sets are bound into three volumes (with the plates at the end of each volume); we have seen one set (in a private library) that has all the text bound in one volume, and all the plates bound in a second volume.

The *Abbildungen* remains of significance today for its new taxa and its extensive, detailed illustrations that often can be used to identify the type specimens. The *Abbildungen* was part of a sizable flowering of illustrated conchological books in the 1840s and 1850s in Germany, France, and England (Dance, 1986: 137–142). The other German illustrated conchological series of this period was the second edition of the Martini-Chemnitz *Systematisches Conchylien-Cabinet*, re-started by Heinrich Carl Küster in 1837, and ran for nearly a century before ending in 1920. The *Systematisches Conchylien-Cabinet* similarly had lavish illustrations and extensive descriptions and, as for the *Abbildungen*, had a needlessly complicated issuance of volumes and parts, with some genera being issued in ten or more parts over several decades. The authorship and dates of publication were not fully worked out until long after it ceased publication (Johnson, 1968; Welter-Schultes, 1999). Philippi was the sole author of several lengthy sections of the *Systematisches Conchylien-Cabinet*, particularly *Ampullaria*, *Natica*, *Solarium*, *Trochus*, and *Turbo*, along with shorter treatments of several other gastropod genera, which appeared from 1842 to 1855.

The third German malacological publication that Philippi contributed to arose from his role as one of the founders of the *Zeitschrift für Malakozoologie*, one of the first German malacological periodicals of significance. This journal, edited by Karl Theodor Menke, appeared in 10 volumes from 1844 to 1853, with 12 issues per volume, originally intended to appear on a monthly basis (Kabat & Coan, 2016). Unlike the *Abbildungen* or the *Systematisches Conchylien-Cabinet*, the ten volumes of this journal had only two plates with illustrations (but neither was for Philippi's papers). Starting

in 1847, Philippi authored a series of articles, initially titled as *Testaceorum novorum centuria* [One hundred new shells] (1847–1848), which was then succeeded by the *Centuria altera testaceorum novorum* (1849), the *Centuria tertia testaceorum novorum* (1849), the *Centuria quarta testaceorum novorum* (1849–1851), and finally the *Centuria quinta testaceorum novorum* (1851–1852). In the first through fourth series, the 100 species of each series were numbered 1–100; however, the fifth series ended in 1852 with species number 83 (probably because Philippi was in Chile and no longer able to send descriptions to the editor), for a total of 483 species. The editors remarked in the February 1851 issue, volume 7(9), that Philippi had to leave, perhaps forever, due to the unprecedented political events in Hesse (Menke & Pfeiffer, 1851a: 144). Later that same year, in volume 8(8) (probably published between October and December 1851), the editors remarked at the end of the third part of the *Centuria quinta* (which ended with species number 52), that they hoped that Philippi was now in Chile and would be able to send the next part (Menke & Pfeiffer, 1851b: 126). As it happens, the last part of the *Centuria quinta* was published in volume 9(2) (25 March 1852), but it must have been based on a manuscript that Philippi left behind, as he arrived in Chile in December 1851, which was not enough time to send new manuscripts to Germany.

One problem with the *Zeitschrift* series is that Philippi originally used it as a way to provide preliminary descriptions of species that were later described in greater length and with illustrations in the *Abbildungen* or the *Systematisches Conchylien-Cabinet*. Even though the latter publications have adequately detailed descriptions and figures – often based on additional specimens from other localities not mentioned in the original description – the shorter original descriptions in the *Zeitschrift*, without illustrations and from fewer localities, limit the availability of type material. And, since the descriptions in the *Zeitschrift* continued for another year after the *Abbildungen* ended, that meant that a number of the species described in 1851 and 1852 were never illustrated by Philippi. Further complicating matters is that the German revolution from 1848 to 1851, combined with Philippi's escape to Chile, meant that it was not possible for Philippi to coordinate the timing of these publications (or to review the page proofs), so that while the preliminary description in the *Zeitschrift* usually



came before the more detailed descriptions in the *Abbildungen* or the *Systematisches Conchylien-Cabinet* (as intended), other species were sometimes published first in the latter monographs.

Philippi, before his departure for Chile, and while on board the ship en route to Chile, completed his magisterial *Handbuch der Conchyliologie und Malacologie* (1853). He wrote in the foreword that he completed this book on 18 October 1851 “in der Nähe von Cap Hoorn an Bord der Hamburger Brigg Bonito” [near Cape Horn, on board the Hamburg ship *Bonito*] (Philippi, 1853: vi), but it was not published until early 1853, reflecting the delays in transmitting the manuscript from Chile back to Germany. The *Handbuch* demonstrated Philippi’s vast knowledge across the entire phylum: the first section discussed the history of the classification of molluscs and the diagnostic characters; the second section, of over 340 pages, set forth a comprehensive diagnosis and classification of the entire phylum, down to the family and genus level; and the third section, of 65 pages, comprised a detailed alphabetical index to molluscan genera. The book included brachiopods and ascidians, which were not removed from the Mollusca until later in the 19th century (Hyman, 1959: 516–517; 1967: 2); Philippi listed the rudists, now known to be fossil bivalves, as the third “order” within the brachiopods. Philippi also included barnacles in an appendix; he explained that they were crustaceans, but he included them anyway, since “die meisten Liebhaber die Gehäuse derselben in ihre Sammlungen aufnehmen” [most shell collectors have them in their collections] (Philippi, 1853: v). A significant limitation of this 1853 book, which reduced its impact, was that Philippi included no illustrations (Barros Arana, 1904: 62), in contrast to other detailed surveys of the Mollusca in that same decade, such as H. Adams & A. Adams, *The genera of Recent Mollusca* (1853–1858), with 138 plates. An anonymous reviewer, while praising this work as “an excellent manual, and almost the only work on the subject which approaches the present state of the science,” criticized Philippi for his habit of incorrectly emending the names of genera in order to make the names fit what Philippi believed to be their etymology: “There are many instances where explanations are given of [genus] names which were intended simply as names without any meaning, and some names of this kind are corrected to make

them fit the explanation given!!!” (Anonymous, 1853: 317).

After Philippi’s arrival in Chile, and after his network of collectors and he amassed sizable collections of Mesozoic and Cenozoic fossils of that country, Philippi began describing those fossils. While Darwin and d’Orbigny collected and described a small number of Chilean fossils, their discoveries barely scratched the surface of Chile’s paleontological diversity. Hence, in 1887, Philippi published, in simultaneous German and Spanish editions (albeit with slightly different paginations), *Die Tertiären und Quartären Versteinerungen Chiles / Los fósiles Terciarios i Cuaternarios de Chile*, with the bulk of this work devoted to fossil molluscs (a few fossil vertebrates, as well as various other invertebrates, were also covered). Philippi described 504 new species of fossil molluscs (including 312 bivalves and 181 gastropods) in the 1887 book, of which 350 species are Cenozoic (Nielsen, 2009). Despite its title, the 1887 book also includes 154 species of Cretaceous molluscs (i.e., Mesozoic). Philippi had already described 47 fossil molluscs from Chile in several earlier papers, particularly in the 1860 Atacama survey.

Philippi’s last malacological contribution was the *Los fósiles Secundarios de Chile*, which appeared in 1899, and had 202 new species of molluscs, all bivalves. Despite the title of this work, it was limited to what Philippi termed the “asiphonate” bivalves, that is, primarily the Protobranchia, Mytilidae, Arcidae, Ostreidae and Trigoniidae (thereby excluding the heterodont and anomalodesmatan bivalves), all from the Jurassic. The Cretaceous bivalves were already treated in the 1887 “Tertiary” work, and Philippi never did publish on Triassic bivalves of Chile. At the Museo in Santiago, there are a number of old cabinets filled with hundreds of lots of Jurassic gastropods and heterodont/anomalodesmatan bivalves (particularly of “*Pholadomya*”), labeled with manuscript names, presumably intended to be published in this series, had Philippi’s eyesight not given out due to cataracts (Philippi, 1899: v; 1904: 323). The introduction to this work optimistically predicted that the second volume would cover gastropods and cephalopods, with 40 to 50 plates, and the third volume would cover brachiopods, echinoderms, corals, reptiles, and “problematic” fossils, with 20 plates (Philippi, 1899: vi).

While the 1887 book has recognizable illustrations and descriptions, the 1899 book,



written after his eyesight had deteriorated, is not as well illustrated and the descriptions of new species are often based on worn or indeterminate specimens. For example, a number of his new Jurassic species of "*Pecten*" have been synonymized under *Weyla*, a stratigraphically important genus (Aberhan, 1994). Even more problematic was his description of 69 new species of "*Trigonia*" – many later determined to be referable to other families, such as the Astartidae, Lucinidae and Cardiidae (Pérez & Reyes, 1989).

Taken together, the 1887 and 1899 books, along with his earlier Chilean paleontological publications, included the description of 753 new species of fossil molluscs from Chile. This is assuredly the largest number of new species of fossil molluscs from the Jurassic to Pleistocene that anyone will ever describe from that country. Some of the fossils were collected by Philippi; others were donated by a network of dedicated amateurs, including Luis Landbeck, Jerman Volkmann, Francisco Javier Ovalle Olivares, Guillermo Fonck, Federico Albert, Ramón Vidal Gormáz and [Robert?] MacSporran (Gotschlich, 1914: 258–259), commemorated with species names.

According to Gotschlich (1904: 178–179) and Ochsénus (1906: 66), Philippi, upon his death, left behind at least 35 manuscripts, of which three relate to molluscs: (1) "Catalogus Moluscorum Chilensium;" (2) "Moluscos chilenos" (with 25 plates and over 400 figures); and (3) "El Segundo i tercer tomo de los fósiles secundarios de Chile" or "Chilenische Sekundärpetrefakten, Bd. 2 und 3." The Universidad Austral de Chile, Dirección Museológica (Valdivia), which has some of Philippi's notebooks and archival materials, has several handwritten manuscripts on Chilean molluscs, presumably corresponding to the first and/or second items, as well as a number of Philippi's original watercolors and line drawings (Figs. 5–6) (Muñoz le Breton, 2003). These manuscripts in Valdivia are lists of the genera and species of molluscs found in Chile, with descriptions of each taxon (A. R. Kabat, pers. obs.). Even today, there still is no such comprehensive published work on the Chilean molluscan fauna. The third manuscript was intended to continue the 1899 book on the Jurassic bivalves of Chile, and presumably had one volume on the "higher" bivalves, and one volume on the gastropods and other molluscan classes, but the current location of this potentially important paleontological manuscript is unknown.

## NOTE ON ORTHOGRAPHY

Rudolph Amandus Philippi's first name is sometimes misspelled in the subsequent literature as the German variant "Rudolf." When Philippi emigrated to Chile, he used the Spanish version of his given names when publishing articles or books in Spanish, that is, Rodolfo Amando Philippi. However, in the 1880s–1890s, there was a short-lived movement in Chile to simplify the spelling of Spanish words (Contreras, 1993: 200–203), so that "Zoologia" became "Zoolojia," "Geologia" became "Jeolójia," and "Paleontologia" became "Paleontolójia" (as reflected in the titles of several serials in which Philippi published during that time period). It appears that as a result of this simplified spelling movement, some Chilean sources (but not Philippi himself) rendered Philippi's first name as "Rodolfo" or "Rudolfo" instead of Rodolfo. The otherwise authoritative *Neue Deutsche Biographie* managed to misspell both versions of Philippi's first name, by using "Rudolf (Rudolfo)" (Zirnstern, 2000a: 391).

Chileans follow the Spanish custom by including both parents' last names as part of an individual's family name, but Chile is unique in having the second name typically abbreviated to just the first letter. Although Philippi himself did not follow this custom, some Chilean biographical sources have used "R. A. Philippi Krumwiede" or "R. A. Philippi K." for his name, with the "Krumwiede" being his mother's maiden name (and, confusingly, his wife's maiden name, as he married a first cousin on his mother's side). Castillo Infante et al. (1996: 396) misspelled this as "Krumwide."

## R. A. PHILIPPI'S RELATIVES

R. A. Philippi was not the only Philippi to make significant contributions to natural history. His brother, Bernhard Eunom Philippi (1811–1852), despite his short life, not only played a major role in promoting German emigration to Chile, but also collected numerous molluscs from South and Central America, many of which were described as new species by R. A. Philippi. Sometimes, the publications and museum labels list the collector as "E. B. Philippi" which is a transposition of his given names; other labels list the collector only as "Frater," Latin for brother. Bernhard's (Bernardo's) short life has been amply docu-









FIG. 6. Chilean "Ammonites" plate – probably from the unpublished second and third parts of the "Los fósiles Secundarios de Chile" (reproduced courtesy of the Universidad Austral de Chile (Valdivia), Dirección Museológica).

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FIG. 5. Chilean "Patella" plate, from the unpublished manuscript, "Moluscos chilenos" (reproduced courtesy of the Universidad Austral de Chile (Valdivia), Dirección Museológica).



mented (e.g., Lindgren, 2001; Perich Slater, 1980; Philippi, 1901b; Tampe Maldonado, 1977; Wunder, 1988; Young, 1971), and even inspired a historical novel written for Nazi youth by “Veit Bürkle” (a pseudonym for Karl Heinrich Bischoff, 1900–1978), who ended his histrionic book by describing Bernhard’s murder in Patagonia as his blood sacrifice for the clear and strong German-Chilean friendship (“einer klaren, stolzen deutsch-chilenischen Freundschaft sind, für die Bernardo E. Philippi sein Blutopfer brachte”) (Bürkle, 1938: 246; 1942: 246).

Kay (1979: 25), in her otherwise quite accurate history of shell collecting in Hawaii, wrote that “Two 19th-century travelers of lesser note who visited the Hawaiian Islands were ... and Herr Richard Philippi. ... The shells collected by Philippi, a German merchant who made his fortune and home in Chile, were described by his brother, R. A. Philippi.” Ziegler (2002: 379) repeated this error by listing “Richard Philippi” as an “independent Prussian” naturalist who visited Hawaii. However, we have found no trace of any “Richard Philippi” or any other Philippi who was a wealthy German merchant who settled in Chile. It appears that Kay’s reference should have been to Bernhard (Bernardo) Philippi, who did visit the “Sandwich Islands” during his round-the-world trip in 1830–1831 (Wunder, 1988: 362).

Carl Theodor Philippi (1819–1852), a nephew (i.e., the son of R. A. Philippi’s oldest half-brother, Carl), initially studied theology at the Universität in Berlin, at his father’s demand. But, his father eventually allowed him to switch to botany. Theodor then served as an assistant curator of the herbarium of the Botanisches Museum (Berlin) from 1841 to 1848. He made an extended botanical collecting expedition from 1844 to 1846 to southeast Asia, including India, Burma and China, and also collected a number of marine molluscs from Asia, some of which were described as new species by R. A. Philippi (the museum labels usually list the collector as “Theodor” or “T. Philippi”). Theodor emigrated to Chile in 1849, where he was known as “Teodoro,” briefly serving as professor of natural history at the Instituto Literario de Concepción, which much later became the Universidad de Concepción. However, Teodoro died at the age of 33 of an abdominal ulcer in April 1852, earlier in the same year that Bernhard was killed (Bretschneider, 1898: 373–374; Gunckel Lüer, 1951b; Klotzsch, 1852; Philippi, 1897–1898: 241; Urban, 1881: 121, 148).

Friedrich Heinrich Eunom Philippi (1838–1910), the only one of R. A. Philippi’s children to pursue a career in natural history, was born in Naples, and after co-authoring several entomological papers with his father, devoted the rest of his career to Chilean botany. Friedrich – known as Federico in Chile – never quite escaped his father’s shadow, succeeding him as director of the Museo Nacional de Historia Natural in 1897, but outliving him by only six years, dying in 1910 (Gotschlich, 1910a, 1910b; Henze, 1995a; Jaksic et al., 2012: 88–91). Friedrich was the only one of Philippi’s ten children to have children of his own – five by two marriages – and those five grandchildren, in turn, resulted in Philippi having 23 great-grandchildren and at least 45 great-great-grandchildren by 1960 (Schwarzenberg de Schmalz & Oyarzún Philippi, 1960).

Otto Philippi Westermayer (1866?–1921), a son of Friedrich and a grandson of R. A. Philippi (Figueroa, 1931: 507; Schell, 2013: 187), also studied Chilean botany, and collected a number of type specimens of plants that were described by his father and grandfather (Barnhart, 1965: 80).

Rodolfo Amando Philippi Bañados (1905–1969), a great-grandson and the namesake of R. A. Philippi, and the son of Otto Philippi Westermayer, was a pediatrician in Santiago, known for his interests in ornithology. He published over 60 articles on Chilean birds, and co-authored the multi-volume *Los Aves de Chile*. He served as “Jefe de la Sección Ornitología” (curator of birds) at the Museo Nacional de Historia Natural from 1938 to 1966, and was also assistant director of the Museo from 1963 to 1966 (Drouilly, 1969). Despite these official positions, Philippi Bañados kept his extensive research collection “in his home rather than at the Museum, where he feared for their fate” (Vuilleumier, 1995: 105). At the time of his death, about half of his collection (primarily the small birds that could be easily shipped by mail) was acquired from his widow by the Museum of Comparative Zoology (Harvard University); the rest was subsequently acquired by Manuel Marín Aspillaga, a Chilean ornithologist, who transferred it in the 1980s to the Western Foundation of Vertebrate Zoology (Camarillo, California) (Anonymous, 1969: 42; Kiff, 2000: 203; M. Marín, in litt. 19 Nov. 2015). The irony is that in 1853, R. A. Philippi complained that Claudio Gay had taken all his specimens to Europe, leaving only “junk” in the Museo in Santiago; yet, his great-grandson



Philippi Bañados similarly did not deposit his specimens in the Museo.

Several of R. A. Philippi's other descendants also made important contributions to the development of Chile. Julio Philippi Bihl (1878–1935), another son of Federico and an attorney, collected plants for his father and grandfather as a youth, and then founded what is now one of the largest law firms in Santiago ([www.philippi.cl](http://www.philippi.cl)), and served as a cabinet minister in the Chilean government; his son Julio Philippi Izquierdo (1912–1997), was also an attorney and cabinet minister (Millar Carvacho, 2005). Rodolfo Amando Oyarzún Philippi (1895–1985) (the son of Federico's daughter Isabel), was instrumental in bringing modern architecture and urban design to Chile (Pachecho Barrera, 1988).

Jaime Eyzaguirre Philippi (born 1935), a great-great-grandson of R. A. Philippi, is a professor of biochemistry at the Universidad Andrés Bello (Santiago); his sister, María Teresa Eyzaguirre Philippi (born 1952), a great-great-granddaughter of R. A. Philippi, currently serves as the Presidenta of the Fundación R. A. Philippi de Estudios Naturales, an organization devoted to preserving the natural history of Chile (<http://www.fundacionphilippi.cl>).

Two other researchers also named Philippi are briefly mentioned, to avoid any confusion in the literature, even though they are not directly related to R. A. Philippi. Emil Ludolf Adam Philippi (1871–1910), born in Breslau (now Wrocław, Poland), spent his short career at Jena, where he published on glacial geology, fossil cephalopods of Germany, and the higher-level classification of fossil bivalves; he died while travelling in Egypt (Solger, 1912; Steinmann, 1910).

Rudolf Philippi (1821–1897; first name sometimes misspelled as Rudolph), served as the Prussian State Archivist in Königsberg, East Prussia (now Kaliningrad, Russia) in the late 1800s, and authored several works on the medieval and ecclesiastical history of East Prussia (Krollmann, 1944: 499; Leesch, 1992: 453–454).

Finally, Arturo Issel, in describing molluscs from the Arabian Gulf, stated that the specimens were collected by “F. de Filippi, direttore del R. Museo zoologico di Torino” (Issel, 1865: 387), which refers to the Italian zoologist Filippo de Filippi (1814–1867), one of the earliest Darwinists in Italy. Bosch et al. (1995: 14) erroneously stated that Issel's specimens were “collected ... in the Arabian Gulf by ... R A Philippi,” having confused Philippi with de Filippi.

## PHILIPPI'S CONTRIBUTIONS TO OTHER TAXA

As if describing over 2,500 molluscan taxa were not enough, Philippi also made substantial contributions to the systematics of numerous other animal taxa, as well as plants and fungi. In particular, after his arrival in Chile, Philippi was able to describe species from the entire length of Chile, both those obtained through his own extensive collecting activities and from a number of amateur naturalists, including fellow Germans, throughout Chile. Castro et al. (2006), after enumerating Chile's biodiversity, determined that Philippi described 1,670 currently recognized species of Recent animals, plants and fungi from Chile (not counting species now known to be junior synonyms), representing nearly 6 percent of the known biological diversity of Chile, and that no other biologist described as many currently recognized species from Chile.

### Botany

The most recent calculation is that Philippi described 3,359 species of plants from Chile (of which about 1,017, or 30 percent, are currently recognized as valid), along with three species of fungi (mushrooms) (Muñoz-Schick et al., 2012; Castro et al., 2006: 136–137). Earlier estimates are somewhat higher, for example, 3,720 species (Taylor & Muñoz-Schick, 1994; Muñoz-Schick, 1973) or 3,695 species (Castro & Muñoz-Schick, 2004: 12), but those numbers may include new generic combinations for previously described species, not just new taxa. As early as 1905, other botanists recognized that Philippi had overdescribed the plants of Chile (Reiche, 1905: 75). While in Germany, Philippi was the first to recognize that the coralline red algae, which he placed in *Lithophyllum*, were plants, not animals (Günckel Luer, 1951a: 439–440). Although Philippi is far from the most prolific botanist (i.e., Augustin Pyramis de Candolle is credited with 10,222 new plant species), he is probably among the top 20 botanists in describing new plant species (Lindon et al., 2015: 211; M. S. Vorontsova & E. Williams, in litt. 11 Aug. 2015).

Philippi's botanical type material is primarily located in the herbarium of the Museo Nacional de Historia Natural (Santiago); the herbarium at the Georg-August-Universität Göttingen (Germany) has some of his pre-1850 collections from Germany, Italy and Switzerland (Frahm & Eggers, 2001: 376–377; Wagenitz, 1982:



126), and his coralline algae type specimens are in Leiden, having been borrowed by F. T. Kützing in the 1840s and never returned (Woelkering, 1983a: 167; 1983b: 300–301). Although Claudio Gay (1800–1873) previously described a number of Chilean plants, Gay's locality information and descriptions left much to be desired, so Philippi's contributions did much to establish the foundation for systematic botany in Chile. At the same time, however, Philippi's uncritical approach to describing new plant species was criticized by subsequent botanists:

“Ebensowenig kann ihm der Vorwurf erspart bleiben, daß er manche Spezies auf durchaus unzulängliche, fragmentarische oder unentwickelte Exemplare begründete und über die Unsumme der neu beschriebenen Arten allmählich selbst die Übersicht verlor, und von ihm selbst beschriebene nochmals unter neuem Namen herausgab.”

[He cannot be spared from the accusation that he described species based on quite inadequate, fragmentary, or juvenile specimens, or that he described an enormous number of new species, losing track of the large number, so that he described the same species twice under different names.] (Reiche, 1907: 19; 1934: 33).

At the same time, however, Chilean botanists remain grateful that Philippi's material remained in Chile for their study, in contrast to other European botanists whose Chilean specimens are a continent away: “Por otra parte, los botánicos chilenos debemos agradecer aún hoy día al Dr. Philippi que haya dejado en Chile su material de tipos.” (Gunckel Lüer, 1951a: 440).

The most noteworthy Chilean plant species described by Philippi is *Echinopsis atacamenensis* (Philippi, 1860), the tallest cactus native to Chile, with a height of up to ten meters; the even taller San Pedro cactus, *E. pachanoi*, known for its mescaline, was subsequently introduced to Chile. Interestingly, Louis Pfeiffer, Philippi's malacological colleague in Cassel, also published extensively on cacti (Hesse, 1958: 253), as did Charles Russell Orcutt (1864–1929), a shell collector in California (Coan, 1966).

Philippi also founded the herbarium at the Museo Nacional, and his son Federico, after dabbling in entomology, devoted most of his professional career to botany (Muñoz Schick, 1991: 181–186). Federico's son Otto Philippi Westermayer, in turn, described over 100 new species of plants from Chile and Argentina,

resulting in three generations of Philipps in Chilean botany (Muñoz-Schick et al., 2012: 129; Schell, 2013: 187). Bruggen (2012: 139) recently noted that while he was aware of at least three botanical systematists who went on to make contributions to malacology, “cases of the opposite, viz., mollusk specialists who also made their mark on systematic botany, are as yet unknown to me,” but R. A. Philippi surely qualifies as someone whose first specialization was molluscs and later made significant contributions to botany.

## Entomology

Philippi's 1830 university thesis was on the grasshoppers of Berlin, but he did not return to entomology in depth until after his arrival in Chile. While in Chile, he described some 807 species of insects, mostly dipterans (flies) and coleopterans (beetles), of which about 525 are now considered valid (Camousseight, 2005; Castro et al., 2006: 136–137; Cortés & Herrera, 1989: 306; Pérez, 2004). Philippi also co-authored several entomological papers with his son Federico; the authorship of one was incorrectly rendered by the publisher as “A. H. E. Philippi”, which is an error for F. H. E. Philippi (Camousseight, 2005: 104).

## Other Invertebrates

Philippi also published extensively on numerous other invertebrate groups, both in Europe and in Chile; his work on barnacles and sea urchins is of broader interest. Darwin, in researching his monographs on barnacles, made good use of the fossil specimens described and collected by Philippi and others (including Dunker, F. C. L. Koch and F. A. Roemer) from Germany, as reflected in Darwin's correspondence with Dunker, in which Darwin specifically requested that Dunker send him Philippi's barnacle specimens. In 1850, Darwin wrote to Dunker, “If you could persuade the distinguished Philippi to send me a specimen (allowing me to disarticulate it) of the Mediterranean species which he has named [i.e., *Pollicipes carinatus* Philippi, 1836], it would be doing me the greatest service ...” (Burkhardt & Smith, 1988: 359–360; Portman, 1950: 208). After Darwin published the first part of his monograph on the fossil barnacles, he sent several copies to Dunker, requesting that Dunker send them to the “three distinguished naturalists,” that is, Roemer, Koch and Philippi,



who had all provided specimens to Darwin via Dunker (Burkhardt & Smith, 1989: 12; Portman, 1950: 208). Darwin's monograph thanked those three naturalists, and Dunker, for providing "specimens of great value; and to these most distinguished naturalists I beg to return my very sincere thanks." (Darwin, 1851: vi).

Perhaps the most widely cited invertebrate species described by Philippi is *Diadema antillarum* (Philippi, 1845), the long-spined black sea urchin from the Caribbean Sea, an ecologically important species that prevents algae from overgrowing the coral reefs (Rodríguez et al., 2013).

### Vertebrate Zoology

Philippi published over 40 papers on ornithology (Paynter, 1988: 310–313), and his most noteworthy bird species is the Andean flamingo, *Phoenicoparrus andinus* (Philippi, 1854), one of three flamingo species known from the high elevation Andean altiplano of South America, where it is an ecologically important grazer of diatoms (Bayly, 1993: 229). Philippi's great-grandson, also an ornithologist, discussed Philippi's other new avian taxa, but candidly noted the problems with his inadequate descriptions and lack of comparisons with previously described taxa (Philippi Bañados, 1963: 3).

Philippi's contributions to herpetology were admittedly not up to the standards of his time, let alone the modern era, partly because of his "espíritu apasionadamente critico y polemico" [passionately critical and polemical spirit], which led him to reject the opinions of other herpetologists; although he described some 41 new snake species and eight new snake genera from Chile, all are now junior synonyms and some are not even from Chile (Donoso-Barros & Cardenas, 1965: 225; see also Ortiz & Nuñez, 1986). Similarly, Philippi's 1902 review of Chilean amphibians, an update to Claudio Gay's 1848–1849 review, "unfortunately is replete with error" (Adler, 1989: 64).

Philippi described numerous fish and marine mammals from the Chilean coast (Pequeño Reyes, 2003: 31, 33–35), a region known for its rich, cold-water biodiversity due to the upwelling of the Humboldt Current.

Philippi described several fossil vertebrates from Patagonia, a region known for its rich fauna of extinct mammals, and elsewhere in Chile (Frassinetti, 1982: 21). The most noteworthy are two species of giant ground sloths, *Megatherium medinae* and *M. sundti*, both still recognized as valid (De Iuliis, 2006).

### PHILIPPI'S HERITAGE

Philippi's name lives on not only through his numerous species, but also through the extensive research collections that he built up at the Museo in Santiago. Schell (2013: 228) concluded that this Museo was unique among South American museums in having "almost 90 percent of Chile's type specimens to date," since "the type specimens of most Latin American countries are held in institutions in Europe or the United States, a legacy of formal or informal imperial power." Thus, "thanks to the work of Philippi and his collaborators, Chile holds the library of its own natural history specimens" (Schell, 2013: 228).

In malacology, Philippi's name lives on through the genus *Philippia* Gray, 1847, (Gastropoda: Architectonicidae), which became the basis for the subfamily name Philippinae Melone & Taviani, 1985. Numerous molluscan species were named after Philippi, too many to enumerate here. In botany, at least five genera of plants were named after him: *Philippia* Klotzsch, 1834; *Philippiamra* O. Kuntze, 1891; *Philippicereus* Backeberg, 1942; *Philippiella* Spegazzini, 1897; and *Philippimalva* O. Kuntze, 1891 (Stafleu & Cowan, 1983: 237).

Although Philippi's name also lives on in Chile through the names of schools (including the Deutsche Schule R. A. Philippi/Colegio Alemán R. A. Philippi, founded in La Union in 1860), the Museo de Historia Natural Rodolfo Philippi in Chañaral (Atacama province, a small museum founded in 1982), streets, parks, and even a postage stamp issued in 1978, his greatest legacy in Chile is, of course, the Museo in Santiago and his collections and publications that document Chile's biodiversity.

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THE MALACOLOGICAL CONTRIBUTIONS OF  
RUDOLPH AMANDUS PHILIPPI (1808–1904)

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ABSTRACT

Rudolph Amandus Philippi (known in Chile as Rodulfo Amando Philippi), was one of the longest-lived and most prolific malacologists of the 19th century, as his scientific work began in Germany in the 1830s and continued unabated until his death in Chile in 1904. Philippi contributed significantly to malacology: he described over 2,500 new taxa of Recent and fossil molluscs from around the world (2,528 species, 40 genera and three families), particularly from Italy and Chile, and discussed numerous taxa described by other authors. Philippi initially published primarily on Recent and fossil molluscs from Europe in the 1830s, then expanded to marine molluscs from around the world by the 1840s. In 1851, Philippi escaped the German Revolution by emigrating to Chile, where in 1853 he became the director of what is now the Museo Nacional de Historia Natural (Santiago) and a professor at the Universidad de Chile. Philippi's contributions to malacology after his move to Chile were primarily on the fossil molluscs of Chile. Philippi also made significant contributions to the systematics of numerous other animal taxa as well as in botany. In a companion paper (Kabat & Coan, 2017), we provide an analysis of Philippi's life and scientific contributions. This paper catalogs Philippi's malacological publications and taxa.

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MATERIALS AND METHODS

We reviewed all of Philippi's publications known or likely to discuss molluscs, indexed

the new taxa, and we reviewed the secondary literature to identify relevant subsequent references to Philippi's publications and taxa. To ensure that our coverage of Philippi's taxa was as thorough as possible, we reviewed all the taxa attributed to him in the online, searchable versions of Sherborn (1922–1933), Neave et al. (1939–1996) and Ruhoff (1980). Nearly all of Philippi's malacological and paleontological publications are available online through the Biodiversity Heritage Library or Google Books.

As discussed in our companion paper (Kabat & Coan, 2017), Philippi's autobiography, *Mein Leben: Meine Lebensbeschreibung (nur für meine Kinder)* [*My life: my autobiography (only for my children)*] (Philippi, 1897–98), and several of his manuscript notebooks, particularly one with color illustrations of the marine invertebrates of Sicily, are now housed in the Archivo Emilio Held Winkler, Deutsch-Chilenischer Bund/Liga Chileno-Alemana (Santiago). The Universidad Austral de Chile, Dirección Museológica (Valdivia), also has some of Philippi's manuscripts, including an unpublished catalog on the molluscs of Chile, and his correspondence with naturalists and

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collectors in Chile and elsewhere in the world (Muñoz le Breton, 2003).

One of us (Kabat) has visited the museums known to have Philippi's molluscan collections: Museo Nacional de Historia Natural (Santiago); Museum für Naturkunde (Berlin); Muséum d'Histoire Naturelle, Muséum de Rouen; Muséum National d'Histoire Naturelle (Paris); Natural History Museum of the United Kingdom (London); and Naturmuseum Senckenberg (Frankfurt). These museums had specimens that were already recognized as type material, and searching through the general collections led to the discovery of yet other hitherto unrecognized type specimens.

The measurements of type specimens, when given herein, were made with digital (electronic) calipers. The measurements of gastropods are height (parallel to the shell axis) and width (perpendicular to the shell axis, at the widest part of the aperture), except for the low-spined *Haliotis*, for which the length and width are given. The measurements of bivalves are length (parallel to the hinge line) and height (perpendicular to the length and running through the uppermost point of the hinge line). For most bivalves, the length corresponds to the maximum dimension; for some bivalves with trapezoidal shapes or otherwise diagonally elongated valves, the length may be slightly shorter (by 5% to 10%) than the maximum dimension. In order to compare type material with Philippi's original measurements, it should be noted that in his publications from the 1830s to the 1850s, he used the German Linie (1 Linie = 2.18 mm, indicated by Philippi with a triple-apostrophe, e.g. 4.5''' is 4.50 Linie). This is confirmed by comparison with several of his measured holotypes (M. Huber, in litt., 9 Sept. 2014). In his publications from the 1880s and 1890s, he switched to the metric system, giving measurements in millimeters.

#### HISTORY OF PHILIPPI'S COLLECTIONS

Given Philippi's hasty escape from Germany to Chile in 1851, as well as the damage caused to German collections during World War II, it is remarkable that so much of his collection has survived to the present time. Philippi described material that he himself had collected (primarily in Sicily and the Naples region of southern Italy), but most of his new molluscan taxa were collected by a wide network of colleagues, including his brother Bernhard Eunom Philippi (1811–1852), his nephew Carl Theodor Philippi

(1819–1852), and many other zoological and paleontological collectors.

The natural history museums in Berlin and Frankfurt have a sizable part of Philippi's collection, primarily species that he described before he escaped to Chile in 1851.

Part of Philippi's collection, primarily fossil and Recent molluscs from Sicily, and fossil molluscs of northern Germany, but also including various species that Philippi described from elsewhere in the world, is housed in the Museum für Naturkunde, Humboldt Universität, Berlin, with the Recent molluscs in the Zoologisches Museum, and the fossils in the Paläontologisches Museum (Dietrich, 1960: 255, 268–269). In 1989, 14 lots of type material of 12 species of fossils described from Sicily were borrowed on loan by a researcher, and while the loan was timely returned in 1996 (with all the returned lots checked on the invoice), the specimens themselves were not found in 2013, and apparently were misplaced after their return in 1996. Several other fossil lots either did not have catalog numbers, or they were not fully recorded herein, and are indicated by underlining "\_\_\_" in the species entry.

The Senckenberg Museum (Frankfurt) also has part of Philippi's collection, obtained through a somewhat indirect route. As described more fully in our companion paper, while Philippi was living in Cassel (Hesse, northern Germany), he was part of a network of German conchologists, including Friedrich Carl Ludwig Koch (1799–1852) and Wilhelm Dunker (1809–1885). Philippi exchanged specimens with Koch, Dunker, and the Heidelberg paleontologist Heinrich G. Bronn (1800–1862). The Bronn collection was transferred to the Senckenberg Museum in 1989. Janssen (1993) discussed and illustrated Dunker's type specimens of marine molluscs from Japan from the Bronn collection, but the existence of numerous Philippi syntypes in the Bronn collection was not widely known.

These specimens in Berlin and Frankfurt are well curated, having survived two world wars in the 20th century and several insurrections in the 19th century. Although it is not known to what extent Philippi's type material remained in the Ottoneum, the natural history museum in Cassel (Kassel), that museum was bombed on 22 October 1943 (Coers-Dittmar & Link, 1993: 110, 112), so that any specimens were presumably lost at that time.

Several other museums in Germany have (or formerly had) collections of fossil molluscs from Germany described by Philippi in the



1840s. The Roemer- und Pelizaeus-Museum (Hildesheim) has material that Philippi described from the Oligocene of Freden and Diekholz, Niedersachsen; at least nine species are represented by type material (Janssen, 1978a, b, 1979a, b; Rust, 1999).

According to Koenen (1890: 305; 1892: 861–864, 942–945, 955–959), the types of several fossil gastropod species (*Pleurotoma obesa*, *Trochus camprestris*, *Bulla dilatata*, *B. plicata* and *B. teretiuscula*) were in the Staatliches Museum für Mineralogie und Geologie (Dresden), a museum now affiliated with the Naturmuseum Senckenberg. Philippi described material collected by August Liebegott Sack (1796–1870?) which may still be extant in the Dresden collections, although with some subsequent mixing of labels (R. Janssen, in litt., 9 Feb. 2016). Philippi also described fossils collected by Gustav Ferdinand Heyse (1809–1883) (Ostermann, 1999: 67–74), a collection later obtained by Adolf von Koenen (1837–1915); Koenen's own collection is now in the Geowissenschaftliches Museum, Universität Göttingen, and further study is needed to determine if Philippi's type material is still extant there (R. Janssen, in litt., 9 Feb. 2016).

Philippi (1847-I) stated that nineteen species of fossil gastropods from Magdeburg and Westeregeln (west of Berlin) were from the "Hallisches Museum," now known as the Geiseltal-Museum (or Geiseltal Sammlung), Zentralmagazin Naturwissenschaftliche Sammlungen der Martin-Luther-Universität (Halle an der Saale), and some material may still exist in that collection (R. Janssen, in litt., 9 Feb. 2016).

The Natural History Museum of the United Kingdom (NHMUK, London), has Philippi material from two sources. First, Philippi described a number of new species of marine molluscs, primarily of Littorinidae and Naticidae, from the collection of Hugh Cuming (1791–1865), and Cuming's collection was acquired by what was then known as the British Museum in 1866, after his death.

Second, Julius Reissner, a book dealer and shell collector in Braunschweig, Germany, had acquired part of the Koch collection of molluscs, which included type material described by Philippi, Dunker and other German malacologists. Since the history of the Reissner collection has not been previously published, we set it forth here. In 1923, Reissner wrote to Guy C. Robson (1888–1945), who was then the Keeper (curator) of Mollusca at the British Museum (Natural History). Unfortunately,

Robson's own research interests were on the Cephalopoda, so he was not particularly interested in the Philippi and Dunker shells. The correspondence between Reissner (who wrote in excellent English) and Robson, from 1 February 1923 through 26 April 1923 is now housed in the archives of the Mollusca Section, NHMUK. Reissner explained that he had bought the collection of Georg von Koch (1790–1861), who had acquired the sizable shell collection of his cousin, the conchologist Friedrich Carl Ludwig Koch (1799–1852), a close colleague of Philippi. Reissner further explained that Koch had close relations with numerous conchologists and shell dealers, including "Dunker, Philippi, Pfeiffer, Menke, Bernardi of Paris, Cuming of London and so on," and that Dunker gave Koch many specimens that Dunker had received from Philippi, Pfeiffer and Menke (letter from J. Reissner to G. C. Robson, 1 Feb. 1923). Reissner went on to explain that he was careful to limit his recognition of "typical ones" [= type specimens] to those sent directly by the author to Koch, or Philippi specimens sent by Dunker to Koch, as well as by checking handwritten lists of Dunker, Bernardi and Philippi, by handwritten labels, and by the underlying correspondence.

Robson initially expressed great interest, asking Reissner to send him a sample of the specimens (G. C. Robson letter to J. Reissner, 26 Feb. 1923), and Reissner responded two weeks later, stating that the specimens had been shipped, along with "the whole correspondence exchanged between Messrs Dunker, Bernardi, Landauer, Cuming and Koch, altogether 77 letters," and suggested a price of £65 (then worth about \$298.00) (J. Reissner letter to G. C. Robson, 9 March 1923).

Regrettably, Robson, after consulting with an unnamed, "highly skilled conchologist who is familiar with the historical aspect of the study," decided that only 17 of the 55 species offered by Reissner were worth purchasing, and he offered the much smaller sum of £6 (then worth about \$27.50) (G. C. Robson letter to J. Reissner, 7 April 1923). Presumably because 1923 was when Germany had serious hyper-inflation of its currency – the Deutsche mark was 430 marks to the dollar in 1922; 28,000 marks to the dollar in February 1923, to over four trillion marks to the dollar by November 1923 (Taylor, 2013: 363–370) – Reissner had little choice but to accept this offer, and regretted that Robson did not want to have the correspondence (J. Reissner letter to G. C. Robson, 11 April 1923). The specimens that were acquired are



now catalogued as NHMUK 1923.7.13.1 to 1923.7.13.63, of which the first 17 specimens correspond to what Robson considered to be type material of 13 species. Of those 13 species, eight were Philippi taxa, four were Dunker taxa, and one was described by C. A. Récluz. However, of the eight “Philippi types” only five lots – *Mactra largillierti*, “*Phasianella*” *kochii* [now in *Tricolia*], *Cerithium kochi*, “*Siphonalia*” *alternata* [now in *Aenator*] and *Achatina rhodostoma* are extant and recognized as type material; three other lots are misidentified and probably not type material – *Pecten bernardi*, *Dosinia gruneri* and *Natica bicolor*. Of the 15 lots of “Philippi types” that Robson rejected, nine are known to have type material at other institutions, while six are not known to have any extant types: *Ampullaria sumatrensis*, *Dosinia dunkeri*, *Mactra hians*, *Nassa sturmii*, *Turbo concinnus* and *Zizyphinus dubius*.

It is not known what happened to the remaining Philippi material or the “77 letters” that Robson rejected in 1923. Reissner died in 1942 at the age of 84, during World War II, according to an online history of Braunschweig, which noted that on 10 July 1942, “Schriftleiter Julius Reißner ist im 84. Lebensjahre verstorben.” (Stadtchronik Braunschweig, Einträge für das Jahr 1942, online at: <http://www.braunschweig.de/leben/stadtportraet/geschichte/stadtchronik.html?id4=1942>). As of 1942, the World War II combat had not yet reached Braunschweig, so it appears that Reissner died of old age. However, as there is no modern trace of the type specimens that Robson rejected, Reissner’s remaining shell collection, including the Koch and Philippi material, was lost in the bombing of Braunschweig on 14–15 October 1944, which also destroyed the paleontological collections of the Geologische Institut (Dorn, 1944: 299; Starke, 1995). “Die Sammlung von F. C. L. Koch wurde in der Universität Braunschweig, der sie übereignet war, ein Opfer des Bombenkrieges.” [The collection of F. C. L. Koch in the Universität Braunschweig, to which ownership had been transferred, was destroyed by the war bombing] (W. Krippendorff, in litt., 8 June 2015).

The most interesting, and unexpected, source of Philippi’s type material was a French shell collector, Louis Largilliert (1798–1855), a banker in Rouen, one of the largest cities in Normandy (Girardin, 1855). Largilliert amassed a sizable shell collection and library, along with numerous other natural history specimens, recognized at the time of his death as one of the best shell collections in France (Girardin, 1855: 143). Largilliert, when applying for membership

in the Académie des Sciences, Belles-Lettres et Arts de Rouen, presented a manuscript, “Considérations philosophiques sur la conchyliologie” [Philosophical considerations regarding shells] (Girardin, 1855: 144); unfortunately, no trace of this manuscript is known. Largilliert obtained many of his shells from Jean Baptiste Thomas Médée Cécille (1787–1873), an admiral with the French navy, and who collected shells during his official travels around the world (Boulanger, 1995; Lepage & Buffetaut, 2014). Philippi described numerous new species from material received from Largilliert.

After Largilliert’s death in 1855, the Muséum de Rouen acquired his shell collection from his widow, comprising an estimated 6,000 species (25,000) specimens (Cantor, 1996: 34; Fouray & Lerond, 1978: 40), at a cost of 6,000 French francs, then worth about £240 or \$1,175 (Letter from the Mayor of Rouen to F.-A. Pouchet, 8 May 1855).

Not until this decade was it publicized why Largilliert had reached out to Philippi to describe his new species, instead of relying upon the numerous conchologists in Paris (Lepage & Buffetaut, 2014). Philippi’s unpublished autobiography explained that he learned the reason after his malacological colleague Louis Pfeiffer returned from a trip to Paris:

Er sagte mir, die pariser Conchiliologen stehlen alle, wie die Raben; der grösste Conchiliendieb ist Herr Deshayes dem daher auch jetzt der Zutritt in alle Conchiliensammlungen untersagt ist, und Sie sind ehrlich. Woher wusste aber Herr Largilliert [*sic*], das ich ehrlich war? (Philippi, 1897–98: 199–200).

[He told me that the Paris conchologists all steal, like ravens; the worst shell thief is Mr. Deshayes; therefore now his access is prohibited in all shell collections and you [Philippi] are honest. But how did Mr. Largilliert know that I was honest?]

Largilliert’s candid assessment of Gérard Paul Deshayes (1796–1875) may have been based on the fact that Deshayes, as for some other conchologists of his time, was not as conscientious about returning some specimens to the original collector, in contrast to Philippi, who was careful to return one or more examples of each new species to Largilliert. Recently, Lepage & Buffetaut (2014: 56) speculated that another French conchologist, Sauveur Abel Aubert Petit de la Saussaye (1792–1870), was instrumental in having Largilliert correspond with Philippi instead of with Deshayes and the other conchologists in Paris. French conchologists remained unhappy that Philippi had the



first choice of Largilliert's material, and later denigrated Largilliert for his allegedly "deplorable habit" of sending "shells in a mediocre condition" to "the German naturalist" (Crosse & Debeaux, 1863: 260).

The Muséum de Rouen, in the years after receiving Largilliert's collection, donated parts of that collection to at least three other museums, including the Musée d'Elbeuf (1860), the Musée de Toulouse (1877), and even the Musée de Teheran, Iran (1863); it is not known what specimens were transferred or whether those institutions still have Largilliert specimens (Lepage & Buffetaut, 2014: 54), although the history of the mollusc collections in Toulouse does not mention Largilliert or Philippi (Astre, 1950). Some Largilliert material is now in the Muséum National d'Histoire Naturelle, Paris.

The Largilliert/Philippi type specimens at Rouen appear to have been studied by only a few malacologists: Fritz Haas, then at the Senckenberg Museum (Frankfurt), studied several type specimens of Unionidae, which Philippe Dautzenberg of Paris borrowed for him (Haas, 1930a, b). Markus Huber, then at the Universität Zurich, studied the types of several other bivalve species (Huber, 2010, 2015), and two French researchers studied potential type material of one species of Littorinidae (Lepage & Buffetaut, 2014). In September 2014, one of us (Kabat) studied these specimens, as well as other gastropod species, for this paper.

The remaining major depository of Philippi's type material is, of course, the Museo Nacional de Historia Natural, Santiago, Chile. In addition to having many of the types of the species described by Philippi while he was living in Chile, the Museo also has some of the Recent molluscs that Philippi described while he was still living in Germany, and that he had brought with him to Chile in 1851 (or that his family brought when they came in 1856).

In 1887 – 34 years after starting at the Museo – Philippi arranged for the Chilean government to buy his personal collection of molluscs and some other fossils for 6,000 Chilean pesos, a sizable sum at a time when the Museo's annual budget was only about 1,500 pesos (Schell, 2001: 49–50). This purchase price was equivalent to about £612.50 or U.S. \$2,970.00 (Llona Rodríguez, 2000: 190). However, based on our observations of the Recent and fossil molluscs, it does not appear that Philippi devoted much effort to curating the collection during his decades in Chile.

Subsequent to Philippi's death, the mollusc collections were largely ignored for decades. It

appears that the Recent mollusc collection had only one curator prior to the 1970s – Walter Biese Nickel (1895–1960), a German refugee in the 1930s, who spent about one decade at the Museo (Fuenzalida Villegas, 1960), where he published several of Philippi's manuscript names for Chilean freshwater gastropods. However, Biese Nickel did not appear to have spent much time (if any) curating the collection. From 1945 through the 1950s, Nibaldo Bahamonde Navarro, a specialist on crustaceans, worked at both the Universidad de Chile and the Museo, and established the "Laboratorio de Malacología" at the Museo in 1958 (Letelier, 2002: 16–17). From 1973 to 2014, Sergio Letelier Vallejos was the curator of molluscs, and was instrumental in having the collection transferred to modern storage units. Prior to this study, it was estimated that this collection had at least 2,000 Recent molluscs from the Philippi collection, including about 300 type specimens (Letelier, 1997: 4; Smith-Ramírez, 2004: 6).

The paleontological collections in Santiago were similarly overlooked in the decades immediately following Philippi's death. In the 1950s, the fossil molluscs were studied and apparently recurated by Juan Tavera Jerez (1917–1991), who served simultaneously as acting Chief of the Sección Geología del Museo Nacional de Historia Natural and taught paleontology at the Instituto de Geología de la Universidad de Chile (Pérez, 2011). In 1955, Tavera prepared a manuscript, "*Revisión de colección tipo de Philippi para control de referencias específicas (anotaciones personales)*", which unfortunately is now lost (Tavera, 1955; Pérez, 2011: 9). It appears from the fossil mollusc collection that someone, possibly Tavera, perhaps aided by an assistant, was able to identify and prepare modern labels for numerous type specimens and other Philippi material, and this 1955 manuscript may have been intended as the basis for a longer publication with lectotype designations. Daniel Frassinetti, the subsequent curator, did not know who had prepared these labels or identified the "lectotypes" (S.N. Nielsen, pers. comm. Mar. 2014). As noted in the catalog herein, these labels sometimes incorrectly stated that a given specimen was a lectotype or the holotype, when it was just the figured specimen (i.e., a syntype). For example, citations by DeVries (1997) that certain lots are "the holotype" were not valid lectotype designations (Nielsen, 2013: 48–49).

In the 1970s, two paleontologists began publishing extensively on the Cenozoic marine molluscs of Chile: Vladimir Covacevich Castex



(1944–1997), of the Servicio Nacional de Geología y Minería (Pérez & Rubilar, 2012), and Daniel Ángel Frassinetti Cabezas (1939–2010), curator of invertebrate paleontology at the Museo (Nielsen & Canto, 2011). Their research, along with the ongoing research of several other paleontologists, resulted in determining the modern status of many of Philippi's Cenozoic species (DeVries, 1995; Nielsen, 2009).

Philippi also described land snails collected in Peru by Antonio Raimondi (1826–1890), an Italian geologist who was Philippi's academic counterpart in Peru (Seiner Lizárraga, 2003: 530–532). Some of that type material is extant in the Raimondi collection in the Museo de Historia Natural, Lima (Peru).

### THE INS AND OUTS OF AUTHORSHIP

Authorship of taxa is covered by ICZN Code Article 50 (1999):

"The author of a name or nomenclatural act is the person who first publishes it. ... if it is clear from the contents that some person other than an author of the work is alone responsible both for the name or act and for satisfying the criteria of availability other than actual publication, then that other person is the author of the name or act."

Philippi's works contain examples both of names by others made available in Philippi's publications, and of names coined by other workers but first made available by Philippi himself. Philippi is also considered to be the author of several taxa first published in the papers or books written by other researchers. Previous workers have not always consistently applied these rules, particularly before the current wording of the Code, and their divergent interpretations have lingered in the literature. Moreover, there can be instances that are hard to determine. We have tried to be consistent, and we provide a listing of taxa that have been misattributed to Philippi after the listing of taxa in that family that are really to be attributed to him.

A few examples demonstrate the possibilities:

Philippi's three-volume set *Abbildungen und Beschreibungen* (1842–1851) contained many new taxa. While Philippi was the author of most of the taxa, he also relied on others to provide descriptions, as is clear from the title page of the first volume:

"Mit Beiträgen der [with contributions by] Herrn Anton, Dr. von dem Busch, Dr. Dunker,

Dr. Jonas, Bergrath Koch, Dr. Pfeiffer, [and] Dr. Troschel."

Which contributions are by these other authors is generally made clear in the text, both by the indication of authorship following a species name and generally also by an authorship indication in parentheses after a description.

For example, the first section of his monograph on *Tellina* (1843i) contains the description of *Tellina sericina* by Jonas, as noted both in the species header and by "(Dr. Jonas)" following the description, and this species has been correctly attributed to Jonas in subsequent years, best indicated in synonymies as "Jonas, in Philippi, 1843". The same is the case with *Tellina truncata* Jonas, but some subsequent workers wrongly attributed this species to Philippi himself, so it is noted at the end of our list of *Tellina*, correcting this authorship. This same section contains *Tellina pellucida* by Philippi himself, again indicated by both the header and a closing "(Ph.)". For his own species, however, Philippi did not always include a closing signature.

On the other hand, the second section of this *Tellina* monograph (1844-l) included *Tellina philippii* Anton, but this was indicated as being "in litt.", and the description was signed "(Ph.)", so this species has to be attributed, somewhat awkwardly, as *Tellina philippii* Philippi, 1844, ex Anton ms. There are also examples of descriptions by others in this work with added notes signed by Philippi after an included description authored and signed by someone else. For example, in a later section on *Tellina* (1846k), *T. meyeri* is by Dunker, as indicated in the species header and ending signature, but Philippi signed an added note at the very end. This perhaps resulted in this species having been mistakenly attributed to Philippi by some subsequent authors, so we list this species after the true Philippi species of *Tellina*.

Contrasting examples are found in the monograph on the Limnaeidae by Küster, Dunker & Clessin in the *Systematisches Conchylien-Cabinet* (1841–1886), which contains descriptions by Philippi of four species of *Physa* in 1841, as indicated in the species headers and ending signatures.

It is ironic that two of the molluscan taxa most frequently attributed to Philippi are not, in fact, Philippi names. The commercially important *Ostrea chilensis*, now classified in *Tiostrea*, was first made available by H. G. Küster (1844) as a result of a caption on the issue cover to Lieferung 45 of the *Systematisches Conchylien-Cabinet*, and plate 13 depicting



the species was issued in *Lieferung* 46 (also in 1844). While some authors have listed this as “Philippi in Küster” (Marshall, 2002), the mere listing of this name by Küster, accompanied by a figure, means that under ICZN *Code* Article 50.1 (1999), the authorship should be credited to Küster, 1844. Although not required by the *Code*, it is best to render this as “Küster, 1844, ex Philippi ms.” The text for this species (Küster, 1843–1868: 74–75) was not published until 1868 and clearly indicated this species as being a manuscript name (“Philippi in litt.”). Similarly, the gastropod family name *Xenophoridae* was credited to Philippi (1853a: 185) in ICZN Opinion 715 (1964), although the family name was first made available one year earlier by Troschel (1852), as noted by Bouchet & Rocroi (2001: 177).

#### TYPE MATERIAL

The dispersal of Philippi’s material, compounded by the poor curation of his own collection in the decades immediately after his death, meant that it has not been easy for subsequent authors to determine with certainty whether a given specimen is, in fact, Philippi’s original type material. Additional factors contributed to this problem. First, Philippi did not always label his specimens as “types” and may also have added specimens to the type material lots after the original publication. Second, the dispersal of Philippi’s collection, both before and after he escaped to Chile, meant that his type material was subject to the vagaries of divergent curatorial care in a number of institutions, and to undocumented losses in World War II. Third, while Philippi’s illustrations are often sufficiently precise to allow matching of figures with specific specimens, Philippi did not hesitate to describe new fossils from worn or indeterminate specimens, making it difficult to identify those specimens, let alone determine their modern identity. It should also be noted that the “original” labels associated with Philippi’s material were not necessarily all hand-written by Philippi himself. Because he described so many molluscan taxa, and even more plants and insects, it is possible that his assistants prepared some of the original labels. Other collectors who received specimens from Philippi may have created their own labels, and there are several different handwriting styles on the museum labels.

Several provisions of the *International Code of Zoological Nomenclature* (ICZN, 1999) were

applied in determining the type status of Philippi’s type material. Of course, it must be recognized that the *Code* did not exist in Philippi’s time, so he can hardly be blamed for the fact that his descriptions require careful scrutiny under the current *Code* provisions. Further, the current provisions regarding lectotype designations did not exist until the 1985 edition of the *Code*, so that several authors prior to 1985 inadvertently designated lectotypes by referencing a specimen as the “holotype” when it was one of several syntypes.

ICZN *Code* Article 73.1 (1999), governing holotypes, makes clear that a holotype can only be inferred if the original description is clearly based on a single specimen, or the author used the term “holotype” or “the type.” Philippi did not use the former term, seldom used the latter term in his descriptions, and rarely indicated that a new species was based on a single specimen. When he did, that specimen, if it can be found, is the holotype. Thus, there is almost no such thing as a Philippi “paratype,” which is only used when the original description specified that there was a holotype or “the type” (Article 72.4.5).

If the original description was either expressly based on multiple specimens, or the original description gave no indication as to the number of specimens, then ICZN *Code* Article 73.2 (1999) requires that the type material, if found, be treated as syntypes. Thus, even if only one specimen is extant, it must be treated as a syntype. For some of Philippi’s new species, he indicated that the species was known from more than one locality. Yet other new species had descriptions that clearly referred to multiple specimens, sometimes by contrasting juveniles with adults, or indicating a range of color patterns in specimens. However, the remaining new species had no indication as to the number of specimens, and while they could have been based on only one specimen, any such specimen must be treated as a syntype, not a holotype. Taken together, the majority of Philippi’s new species fall under the *Code*’s Article 73.2, and their type material, if found, must be treated as syntype(s), even if only one specimen is now extant.

The ICZN *Code*’s provisions governing lectotypes have proven particularly problematic for researchers and curatorial staff. Prior to the 1980s, it was common for subsequent revisers to identify the figured specimen as the “holotype,” and the remaining specimens as “paratypes.” For Philippi’s new species, such an act would be incorrect, since the only Philippi species for which there are holotypes



are those that were clearly based on a single specimen. For those authors who published prior to 2000, ICZN *Code* Article 74.5 (1999) provides that the use by a subsequent author of the term “holotype” is not a valid lectotype selection “when the original work reveals that the taxon had been based on more than one specimen ... unless the author, when wrongly using that term, expressly indicated that he or she was selecting from the type series that particular specimen to serve as the name-bearing type.” In contrast, ICZN *Code* Article 74.6 (1999) provides that if “it has been accepted that a nominal species-group taxon was based on a single specimen and the original description neither implies nor requires that there were syntypes, and if it is considered subsequently that the original description was based on more than one specimen” (emphasis added), then a pre-2000 citation of a specimen as the “holotype” is a valid lectotype designation.

Finally, for lectotype designations made after 1999, ICZN *Code* Article 74.7 requires even greater specificity in the designation, but that only affects a few species herein. It should be noted that ICZN *Code* Article 74.7.3 was amended in 2003 (retroactively to 1 January 2000) to require that such lectotype designations “contain an express statement of deliberate designation (merely citing a specimen as ‘lectotype’ is insufficient).” (ICZN Declaration 44, 2003). ICZN Recommendation 74G was also added in 2003, to make clear that for lectotypes, “The designation of lectotypes should be done as part of a revisionary or other taxonomic work to enhance the stability of nomenclature, and not for mere curatorial convenience.” (Article 75.2 similarly prohibits neotype designations as a matter of convenience.)

As will be seen in the catalog below, the current provisions of the ICZN *Code* have rendered invalid the statements by a number of pre-1980 authors that a certain specimen was the “holotype” of a Philippi species, while treating such statements for yet other species as lectotype designations.

Just as it is no longer considered routine to designate a lectotype in the absence of a need to clarify the concept of a species, it is no longer routine to “restrict”, “designate” or clarify a type locality when the original was broadly stated or unknown. (The term “clarify” is used in Recommendation 76A of the present *Code*.) In the cases of several Philippi taxa, subsequent authors in the 1950s and 1960s made such “restrictions”, as was then routine. However,

now it is often prudent to clarify a type locality when the original locality was unknown, and important to do so when it was incorrect. Such restrictions are often invalid because the type locality is tied to the primary type(s) under ICZN Article 76.1 (1999). These tasks are best done in the context of revisionary work, and we have not done so in this paper.

## TYPE LOCALITIES

Philippi’s publications varied significantly in terms of the quality of geographical and geological (stratigraphical) data provided for his new species. Although Philippi did not hesitate to describe new marine molluscs based on material from unknown localities, most of his new species were accompanied by at least some locality data. The species described in his Sicily books (1836, 1844), which were mostly collected by himself, are usually accompanied by relatively precise locality data, which have been compiled by Greco & Lima (1974: 7–16) and Greco (1986: 13–46).

For localities in Chile, the detailed gazetteers of Muñoz Pizarro (1960: 169–177) and Paynter (1988) are invaluable in identifying and reconciling old place names.

## BIBLIOGRAPHIC NOTES ON PHILIPPI’S *ABBILDUNGEN UND BESCHREIBUNGEN*

As discussed in our companion paper, Philippi authored a three-volume illustrated work on molluscs, with very accurate color illustrations of the new species, the *Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien* (Philippi, 1842–1851). This work can be difficult to cite and to attribute for authorship, for several reasons. First, at least ten other malacologists – Hermann Eduard Anton; Gerhard von dem Busch; Wilhelm Bernard Rudolph Dunker; Israel Heymann Jonas; Friedrich Carl Ludwig von Koch; Christian Ferdinand Friedrich von Krauss; Johann Karl Megerle von Mühlfeld; Karl Theodor Menke; Ludwig Parreyss; and Louis Carl Georg Pfeiffer – are known to have contributed the descriptions of new species, which are properly credited as “\_\_ in Philippi, 18\_\_” but should not be treated as Philippi’s own taxa.

Second, Philippi was the first to make available a number of manuscript names, both of these ten malacologists, as well as several



others (Henry Adams; William Henry Benson; Heinrich Georg Bronn; Imre Frivaldszky; and J. C. Meder), so that those species should be attributed to “Philippi, 18\_\_, ex \_\_ ms.”

Third, the treatments of individual genera were not published as single chapters, but

were often issued in multiple parts, sometimes spread across two or even all three volumes, with dual pagination used to indicate both pagination of each volume as a whole and pagination for the sections covering each genus.

| Volume/<br>Date title p. | No. | Volume<br>pagination                                           | Printed<br>date(s)                                                               | Likely<br>issue date          |
|--------------------------|-----|----------------------------------------------------------------|----------------------------------------------------------------------------------|-------------------------------|
| 1 / 1845                 | 1   | 1–20                                                           | August 1842                                                                      | August 1842                   |
|                          | 2   | 21–46                                                          | February & March 1843                                                            | March 1843                    |
|                          | 3   | 47–75                                                          | November 1843                                                                    | November 1843                 |
|                          | 4   | 76–102                                                         | January 1844                                                                     | January 1844                  |
|                          | 5   | 103–129                                                        | March & April 1844,<br>but a preceding <i>Tellina</i><br>section dated June 1844 | June 1844                     |
|                          | 6   | 130–150                                                        | June & July 1844                                                                 | July 1844                     |
|                          | 7   | 151–178                                                        | October & November 1844                                                          | November 1844                 |
|                          | 8   | 179–204, title p., [2] pp.<br>introduction, [viii] pp. Regist. | December 1844 &<br>January 1845                                                  | January 1845                  |
| 2 / 1847                 | 1   | 1–32                                                           | none                                                                             | September 1845                |
|                          | 2   | 33–63 [64 blank]                                               | October 1845                                                                     | October 1845                  |
|                          | 3   | 65–87 [88 blank]                                               | February 1846                                                                    | February 1846                 |
|                          | 4   | 89–121 [122 blank]                                             | August 1846                                                                      | August 1846                   |
|                          | 5   | 123–152                                                        | October 1846                                                                     | October 1846                  |
|                          | 6   | 153–182                                                        | January & February 1847                                                          | February 1847                 |
|                          | 7   | 183–212                                                        | March 1847                                                                       | March 1847                    |
|                          | 8   | 213–231,<br>title p., [viii] pp. Regist.                       | April 1847                                                                       | April 1847                    |
| 3 / 1851                 | 1   | 1–29 [30 blank]                                                | August & September 1847                                                          | September 1847                |
|                          | 2   | 31–50                                                          | November 1847                                                                    | November 1847                 |
|                          | 3   | 51–81                                                          | February 1848                                                                    | February 1848                 |
|                          | 4   | 1–28<br>[numbering started over]                               | January 1849                                                                     | January 1849                  |
|                          | 5   | 29–61 [62 blank]                                               | March & April 1849                                                               | April 1849                    |
|                          | 6   | 63–88                                                          | October 1849                                                                     | October 1849                  |
|                          | 7   | 89–114                                                         | April 1850                                                                       | April 1850                    |
|                          | 8   | 115–138<br>title p., [1] p. Vorrede,<br>[vi] pp. Regist.       | September & November 1850                                                        | November 1850<br>January 1851 |

Note that the page numbers were not printed on the first pages of each section. In volume 3 after page 81, the main page number sequence was stopped and restarted. Many but not all parts were dated with the month and year, but this collation assumes that each part was issued no sooner than the last dated monograph section included in that part.



PHILIPPI'S MOLLUSCAN TAXA

Philippi described a total of 2,528 molluscan species in five molluscan classes:

| Class          | Number of Species | Species with Type Material located | In %  |
|----------------|-------------------|------------------------------------|-------|
| Polyplacophora | 6                 | 2                                  | 33.33 |
| Scaphopoda     | 11                | 4                                  | 36.36 |
| Cephalopoda    | 6                 | 3                                  | 50.00 |
| Bivalvia       | 1,026             | 446                                | 43.47 |
| Gastropoda     | 1,479             | 403                                | 27.25 |
| TOTAL          | 2,528             | 858                                | 33.94 |

About one-half of Philippi's species were described in five sets of publications – (1) the 1836 and 1844 Sicily books; (2) several papers in the 1840s on the fossils of northern Germany; (3) the 1887 book on Cretaceous and Cenozoic fossils of Chile; (4) the 1899

book on the Jurassic fossil bivalves of Chile; and (5) several other publications on Chilean fossils. The remaining 1,281 species were mostly described in the *Zeitschrift für Malakozoologie* and the *Abbildungen und Beschreibungen*.

| Class          | Sicily books | German fossils | 1887 Chile fossils | 1899 Chile fossils | Other Chile fossil | Recent other sources |
|----------------|--------------|----------------|--------------------|--------------------|--------------------|----------------------|
| Polyplacophora | 3            | 0              | 2                  | 0                  | 0                  | 1                    |
| Scaphopoda     | 2            | 0              | 7                  | 0                  | 0                  | 2                    |
| Cephalopoda    | 1            | 0              | 2                  | 0                  | 3                  | 0                    |
| Bivalvia       | 103          | 38             | 312                | 202                | 37                 | 334                  |
| Gastropoda     | 238          | 109            | 181                | 0                  | 7                  | 944                  |
| TOTAL          | 347          | 147            | 504                | 202                | 47                 | 1,281                |

The table below shows that types are not equally extant for each category of Philippi's publications. The two Chilean fossil books have the highest percentage of species represented by types. The 1836/1844 Sicily books and the Recent molluscs described in other publications have about one-third and one-fourth, respectively, of their species represented by types.

The German fossils are particularly under-represented by type material, partly due to lack of study of the collections of several regional museums, and partly due to losses during World War II. Given the vicissitudes of Philippi's collections and the museums housing them, it is remarkable that so many types are still extant. These numbers include 24 neotypes:

| Publication Category  | Number of Species | Species with Types | In %  |
|-----------------------|-------------------|--------------------|-------|
| Sicily                | 347               | 113                | 32.56 |
| German fossils        | 147               | 15                 | 10.20 |
| Chile 1887            | 504               | 336                | 66.67 |
| Chile 1899 (Jurassic) | 202               | 91                 | 45.05 |
| Chile fossils other   | 47                | 8                  | 17.02 |
| Recent (non-Sicily)   | 1,281             | 295                | 23.03 |
| TOTAL                 | 2,528             | 858                | 33.94 |



Philippi's taxa were not randomly distributed across the Mollusca, but were concentrated in several families, particularly those with excellent fossil records. Five families accounted for one-fourth (24.7%) of his new species: Trochidae (202); Veneridae (144); Naticidae (105); Littorinidae (88); and Mactridae (85). Ten families accounted for over one-third (37.4%) of his new species: the aforementioned five families, along with the Pectinidae s.l. (73); Mytilidae (67); Buccinidae (62); Arcidae (61); and Tellinidae (57).

In the following list, all the molluscan taxa described by Philippi are listed organized as well as we can determine by their current family status mainly based on subsequent literature. Following the true Philippi taxa, this list includes taxa that have been misattributed to Philippi, indicating their correct authorship.

In many instances, Philippi employed broad generic definitions. For example, he included within the bivalve genus *Nucula* members of the Nuculidae, Nuculanidae, Malletiidae and Yoldiidae. Similarly, his use of *Trochus* encompassed members of the Trochidae, Turbinidae and Calliostomatidae. Given the many taxa involved, living and fossil, and the broad geographic scope of his work, we have undoubtedly missed some relevant literature. We have generally refrained from adding our own interpretations.

The Index at the end of this paper will allow location of each taxon.

In his early publications, particularly his books on Sicily (1836a, 1844g), Philippi used the Latin term "mihi" ["I" or "me"] to indicate a transfer of someone else's species from its original genus to another. Some workers have misinterpreted these as new species, and such misinterpretations are indicated here.

In the Introduction above, we discuss the problem of "In's" – when taxa are by Philippi in the works of others and vice versa. We have tried in the list below to consistently apply appropriate criteria, and we also note what we consider to be past incorrect interpretations.

When Philippi treated his earlier taxa in his later works, these references are included; they often add more detailed descriptions, additional localities, and/or illustrations. Yet, there are instances when his earlier species are unexpectedly not mentioned in his later monographs of those families, as well as instances when he used the same new name for a different species in the same family.

Philippi capitalized species names based on surnames. These are here normalized to lower

case. Other orthographic changes, including subsequent spelling changes or misspellings by Philippi or others, are noted in "as" clauses.

In the Sicily books (1836a, 1844g), Philippi included many trinomials, many explicitly as morphological varieties – example: "var.  $\epsilon$  [epsilon] *gracilis*" – which we might not have listed. However, some of these were subsequently treated as subspecific names [ICZN Code Article 45.6.4 (1999)], so we have listed those that were subsequently made available.

Philippi variously used the endings "i" or "ii" for taxa honoring other workers. Whatever he used in the original is the correct spelling [ICZN Code Article 33.4 (1999)], but subsequent publications may have added or subtracted an "i".

The Sicily books (1836a, 1844g) were entirely in Latin, including the place names. To avoid clumsy pedantry, we have translated these into present-day names. Other place names, particularly those in Chile, are as in the original, and we have not attempted to track down localities that may have changed names over the subsequent century. Needless to say, like many other workers of his day, Philippi named some taxa that came from unknown localities. Philippi sometimes gave a museum depository or the name of the collector(s), which we have included, as that can facilitate the identification of type material.

Philippi sometimes renamed homonyms, including both his own and those of others. In some cases, his new names have themselves proved to be preoccupied by junior homonyms. In some cases, he used the terminology appropriate for renaming a homonym when in fact he was proposing a new species based on a subsequent treatment of an older name for a different species. We have endeavored to make a clear distinction between these new species and the actual renaming of homonyms.

This catalog lists over 100 Philippi species names that are now known to be junior homonyms, some of which have already been renamed, or have been replaced by a senior or junior synonym, or are *nomina dubia*. At least 14 of these are Philippi's homonyms of his own earlier-described species (six of these have already either been renamed or otherwise have a synonym that can be used in their place). Philippi obviously did not keep track of his own species names, and there were no comprehensive nomenclators available for him to check before describing new taxa. There are at least 60 other junior homonyms that have not yet been resolved, whether through renaming, or replacement by a junior or senior synonym,



or being treated as *nomina dubia*. There are also eight species where Philippi's name is the senior homonym of another author's name that is in current use, and specialists in those groups will need to determine whether the junior homonym either requires renaming or should be conserved under ICZN Code Article 29.3 (1999). Also, two of Philippi's genera, both fossils, are junior homonyms and would require renaming if they are to be used as valid taxa – *Plagia* Philippi, 1899 [Bivalvia: Bakevillidae], *non* Meigen, 1838 [Insecta], and *Dicolpus* Philippi, 1887 [Gastropoda, *incertae sedis*], *non* Gerstaecker, 1884 [Insecta].

Philippi started out with a fairly conservative use of genera. Subsequently, he began to use other generic names, including those he coined. An odd case is his use of the generic name *Melania*. He first used this name for pyramidellids (marine gastropods), such as *Melania rufa* Philippi, 1836a, now *Turbonilla rufa* (Philippi, 1836). By 1842, he began to use *Melania* for freshwater cerithioideans.

For type species designations of genera, we have applied Articles 66 to 70 of the ICZN Code (1999). Species that were originally designated as the type species of a genus are indicated by (OD); those that were subsequently designated as the type species are indicated by (SD); and those that are the type species by monotypy are indicated by (M).

#### INSTITUTIONAL ABBREVIATIONS AND ACRONYMS

|        |                                                                                                           |
|--------|-----------------------------------------------------------------------------------------------------------|
| AMS    | Australian Museum, Sydney, Australia                                                                      |
| ICZN   | International Code of Zoological Nomenclature (1999)                                                      |
| MAS    | Museo de Ciencias Naturales y Antropológicas "Prof. Antonio Serrano," Parana, Entre Ríos, Argentina       |
| MCZ    | Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.                       |
| MLP    | Museo de Ciencias Naturales de La Plata, Argentina                                                        |
| Muséum | Museum d'Histoire naturelle, Musée de Rouen, France                                                       |
| MNHN   | Museum National d'Histoire Naturelle, Paris, France                                                       |
| MNHNS  | Museo Nacional de Historia Natural, Santiago, Chile (zoological collections); see also below under SGO.PI |

|        |                                                                                                              |
|--------|--------------------------------------------------------------------------------------------------------------|
| NHMUK  | Natural History Museum of the United Kingdom [formerly BMNH, British Museum (Natural History)], London, U.K. |
| NMSA   | Natal Museum, Pietermaritzburg, South Africa                                                                 |
| PHB MB | Paläontologische Sammlungen, Museum für Naturkunde Berlin, Germany                                           |
| RPMH   | Roemer- und Pelizaeus-Museum Hildesheim, Germany                                                             |
| SBMNH  | Santa Barbara Museum of Natural History, Santa Barbara, California, U.S.A.                                   |
| SGO.PI | Museo Nacional de Historia Natural, Santiago, Chile (paleontological collections)                            |
| SMF    | Senckenberg Museum, Frankfurt, Germany                                                                       |
| SNGM   | Museo Geológico del Servicio Nacional de Geología y Minería de Santiago, Chile                               |
| USNM   | National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.                         |
| ZMB    | Zoologisches Museum, Museum für Naturkunde Berlin, Germany                                                   |
| ZRC    | Zoological Reference Collection, Department of Zoology, National University of Singapore                     |

#### POLYPLACOPHORA

*argyrostictus*, *Chiton* – Philippi, 1845i: 59; 1860a: 179 [1860b: 160]. Strait of Magellan, Chile. *Tonicia argyrosticta* (Philippi, 1845) (Dall, 1909: 247; Ramírez et al., 2003: 258). Possible senior synonym of *Tonicia lebruni* Rochebrune, 1884 (Castellanos, 1988: 22 (who had the synonymy reversed); Kaas & Van Belle, 1998: 22, 108).

*deperditus*, *Chiton* – Philippi, 1887a: 104 [1887b: 98–99], pl. 13, fig. 18. Coquimbo, Chile; Tertiary.

*polii*, *Chiton* – Philippi, 1836a: x, 106–107, *non* Deshayes, 1833; 1844g: 83. Sicily, Italy. Synonym of *Lepidochitona corrugata* (Reeve, 1848) (Sabelli et al., 1990: 117; Kaas & Van Belle, 1998: 146). *Chiton polii* Philippi is the type species (OD) of *Middendorffia* Dall, 1882 [often misspelled as *Middendorffia* – ICZN Code Art. 32.2 (1999)], ex Carpenter ms [new name for *Dawsonia* Dall, ex Carpenter ms, 1882, *non* Hartt, 1868, and others], a synonym of *Lepidochitona* Gray, 1821. Syntypes, ZMB 13113 (n = 5) (Sicily, ex Philippi).



*pulchellus*, *Chiton* – Philippi, 1844g: 83, pl. 19, fig. 14a–c, *non* Gray, 1828. Naples, Italy. Synonym of *Chiton (Rhyssoplax) corallinus* (Risso, 1826) (Kaas & Van Belle, 1998: 151).

*variegatus*, *Chiton* – Philippi, 1836a: x, 107–108; 1844g: 83, 301, pl. 19, fig. 13a, 13b. *non* Röding, 1798, *non* Blainville, 1825. Palermo, Sicily, Italy. Synonym of *Lepidochitona cinerea* (Linnaeus, 1767) (Sabelli et al., 1990: 117; Kaas & Van Belle, 1998: 195). Type species (M) of *Adriella* Thiele in Troschel & Thiele, 1893, now a synonym of *Lepidochitona* Gray, 1821. Syntype, ZMB 13118 (n = 1) (Sicily).

*vetustus*, *Chiton* – Philippi, 1887a: 104 [1887b: 99], pl. 13, fig. 19. Coquimbo, Chile; Tertiary.

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“*Acanthochitus*” – Philippi, 1844g: 83. A misspelling of *Acanthochites* Risso, 1826.

#### SCAPHOPODA

*Cadulus* – Philippi, 1844g: 209. Type species (M): *Dentalium ovulum* Philippi, 1844. Pleistocene–Recent, Mediterranean.

*araucanum*, *Dentalium* – Philippi, 1887a: 107 [1887b: 101–102], pl. 12, fig. 17. Lebu, Chile; Francisco J. Ovalle; Tertiary (Steiner & Kabat, 2004: 564). SGO.PI.232, 243 (from Navidad and thus not type specimens).

*dilatatum*, *Dentalium* – Philippi, 1887a: 105 [1887b: 99], pl. 12, fig. 13. “Tumbez”, Chile; Francisco Javier Ovalle; Cretaceous (Steiner & Kabat, 2004: 584).

*gayi*, *Dentalium* – Philippi, 1887a: 107 [1887b: 101], pl. 12, fig. 19. Matanzas & Curauma, Chile; Tertiary (Steiner & Kabat, 2004: 593–594). Syntypes, SGO.PI.241 (Matanzas, n = 1; labeled as “holotipo”); SGO.PI.226 (Curauma, n = 1). Synonym of *Dentalium sulcosum* G. B. Sowerby I, 1846 (Ortmann, 1902: 157, 159).

*gracile*, *Dentalium* – Philippi, 1887a: 107 [1887b: 101], pl. 12, fig. 15, *non* Hall & Meek, 1855, *non* Jeffreys, 1860, *non* Moore, 1866. Navidad, Chile; Tertiary [Miocene]. *Nom. nov.*: *Dentalium navidadense* Pilsbry & Sharp (1898: 210). *Dentalium philippi* Cossmann, 1907, additional unnecessary replacement name, and itself *non* Chenu, 1843, and *non* Monterosato, 1872 (Steiner & Kabat, 2004: 596, 630).

*hyalinum*, *Dentalium* – Philippi, 1846h: 55. Mazatlán, Sinaloa, Mexico. Possible synonym of *Dentalium (Graptacme) semipolitum* Broderip & G. B. Sowerby I, 1829 (Keen, 1971: 886).

*lebuense*, *Dentalium* – Philippi, 1887a: 106–107 [1887b: 101], pl. 12, fig. 18. Lebu & Llancahue, Chile; Tertiary (Steiner & Kabat, 2004: 609). Syntypes, SGO.PI.224 (n = 1), SGO.PI.4684 (n = 1), SGO.PI.4685 (n = 2), all from Lebu.

*ovulum*, *Dentalium* – Philippi, 1844g: 208–209, pl. 27, fig. 21, 21a. Crotone, Calabria, Italy; Pleistocene. The Pleistocene and possibly Recent Mediterranean *Cadulus ovulum* (Philippi, 1844); type material not located (Sabelli et al., 1990: 342; Steiner & Kabat, 2004: 625). Type species of *Cadulus* Philippi, 1844 (q.v.).

*parvulum*, *Dentalium* – Philippi, 1887a: 107–108 [1887b: 102], pl. 12, fig. 16. Navidad & Lebu, Chile; Tertiary. *Dentalium philippianum* Pilsbry & Sharp (1898: 212), replacement name for “*Fistularia parvula* (Philippi), *non* *Fistularia parvula* Stoliczka, 1868”. Although the two are now regarded as belonging in different genera, Philippi’s original name cannot be restored (ICZN Code Article 59.3 (1999)). Syntypes, SGO.PI.228 (Navidad, n = 1, labeled as “lectotipo”); SGO.PI.4686–4696 (Navidad, labeled as “paralectotipo”); SGO.PI.230 (Lebu, n = 1).

*pusillum*, *Dentalium* – Philippi, 1836a: xiv, 245; 1844g: 208. Palermo & Catania, Sicily, Italy. *Nomen dubium*; possibly a polychaete (Steiner & Kabat, 2004: 635, 668).

*subcylindricum*, *Dentalium* – Philippi, 1887a: 105 [1887b: 99], pl. 12, fig. 14. Algarrobo & San Vicente, Chile; Cretaceous (Steiner & Kabat, 2004: 650). Syntypes, SGO.PI.237 (Algarrobo, n = 1, labeled as “lectotipo”); SGO.PI.4683 (Algarrobo, n = 1, labeled as “paralectotipo”).

*texasianum*, *Dentalium* – Philippi, 1849h: 144; 1849z5: 454. Galveston, Texas; Römer. Synonym of *Paradentalium americanum* (Chenu, 1843); type material not located (Steiner & Kabat, 2004: 656).

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“*sulcosum*,” *Dentalium sensu* Philippi, 1887a: 106 [1887b: 100] *non* G. B. Sowerby I, 1846; *D. matanzasense* Ihering (1907: 224), replacement name for Philippi’s misidentification (Parodiz, 1996: 239).



## CEPHALOPODA

- aegoceros*, *Ammonites* – Philippi, 1860a: 142 [1860b: 125], Petref. Pl. 2, figs. 2, 3. Desierto de Atacama, Chile [fossil].
- araucanus*, *Nautilus* – Philippi, 1887a: 33 [1887b: 30], *nomen nudum*. Navidad, Lebu, Llancahue, Chile [fossil]. "Syntypes", SGO.PI.857 (n = 3 fragments), but a nude name cannot have type material. Probable synonym of *Aturia cubaensis* (Lea, 1841), Cenozoic (Nielsen et al., 2009: 76).
- atacamensis*, *Ammonites* – Philippi, 1860a: 142 [1860b: 125], Petref. Pl. 1, figs. 1, 2. Desierto de Atacama, Chile [fossil]. Holotype, SGO.PI.6836. Jurassic, but its current generic placement requires further research (C. Salazar, pers. comm., 25 Feb. 2014).
- magellanicus*, *Nautilus* – Philippi, 1887a: 33 [1887b: 30], *nomen nudum*. Tierra del Fuego, Chile [fossil]. Probable synonym of *Aturia cubaensis* (Lea, 1841), Cenozoic (Nielsen et al., 2009: 76, 81).
- maldonadi*, *Nautilus* – Philippi, 1897: 365–366, pls. 1, 2. S. of Punta Zorra, Isla Chiloé, Chile [fossil]. Synonym of the Miocene *Aturia cubaensis* (Lea, 1841); holotype lost; SGO.PI.6421, neotype (Nielsen et al., 2009: 76, 79, fig. 3A, B).
- rubens*, *Sepia* – Philippi, 1844g: 203. Sicily, Italy. Synonym of *Sepia orbignyana* Férussac in d'Orbigny, 1826 (Sabelli et al., 1990: 343).

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- "*Tremectopus*" – Philippi, 1844g: 201. Spelling error for *Tremoctopus* Delle Chiaje, 1830.
- "*darwini*, *Puzosia*" – Steinmann, 1895: 73–74, pl. 5, fig. 3, text-fig. 4, ex Philippi ms. This species was listed by Wilckens (1904: 272) and Tavera Jerez (1942: 587) as a Philippi species, but it was a manuscript name used by Steinmann. *Kitchinites darwini* (Steinmann, 1895), Maastrichtian, Quiriquina Formation, Chile (Salazar et al., 2010: 200–202).
- "*quiriquinae*, *Pachydiscus*" – Steinmann, 1895: 74–79, pl. 6, fig. 3, text-fig. 5, ex Philippi ms. This species was listed by Wilckens (1904: 272), Paulcke (1906: 232 [66]) and Tavera Jerez (1942: 587) as a Philippi species, but it was a manuscript name used by Steinmann. Synonym of *Menuites fresvillensis* (Seunes, 1890), Maastrichtian, Quiriquina Formation, Chile (Salazar et al., 2010: 214–216).
- "*subplicatus*, *Nautilus*" – Steinmann, 1895: 65–68, pl. 4, figs. 1–3, ex Philippi ms. This species was listed by Wilckens (1904: 272)

and Durham (1946: 428) as a Philippi species, but it was a manuscript name used by Steinmann. Synonym of *Eutrophoceras dorbignyanum* (Forbes in Darwin, 1846), Maastrichtian, Quiriquina Formation, Chile (Nielsen & Salazar, 2011).

## BIVALVIA

## Nuculidae

- amblyrrhyncha*, *Nucula* – Philippi, 1887a: 197 [1887b: 190], pl. 41, fig. 3. Mouth of Río Rapel, Chile; Tertiary. *Nomen dubium*, possibly referable to the Nuculanidae (Villarroel & Stuardo, 1998: 171).
- andina*, *Nucula* – Philippi, 1899: 60, pl. 26, fig. 8. Portezuelo del Tinguiririca, Chile; Frid. Albert; Mesozoic. *Nomen dubium* (Villarroel & Stuardo, 1998: 170), or a species of *Nuculana* (Villarroel & Stuardo, 1998: 171, who erroneously listed this species twice).
- angusta*, *Nucula* – Philippi, 1887a: 193 [1887b: 186], pl. 41, fig. 13. Algarrobo, Chile; Cretaceous. Syntype, SGO.PI.624 (n = 1 valve, labeled as "holotipo"). *Nomen dubium*, possibly referable to the Nuculanidae (Villarroel & Stuardo, 1998: 171).
- apicina*, *Nucula* – Philippi, 1887a: 193 [1887b: 186], pl. 41, fig. 19. "Tumbez", Chile; Cretaceous. Synonym of *Nucula ceciliana* (d'Orbigny, 1842) [proposed as *Mactra*] (Wilckens, 1904: 228–230, pl. 19, fig. 5; Villarroel & Stuardo, 1998: 163).
- araucana*, *Nucula* – Philippi, 1887a: 198 [1887b: 191], pl. 41, fig. 7, 7b. Lebu & perhaps Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.304 (n = 1, Lebu, labeled as "paralectotipo"); SGO.PI.323 (n = 1, Lebu); SGO.PI.336 (n = 1 valve, Navidad). Nielsen & Valdovinos (2008: 203) determined that the records attributed to this species by Villarroel & Stuardo (1998: 165, figs. 142–143) were actually *Ennucula grayi* (d'Orbigny, 1846). *Nucula araucana* is a synonym of *Nucula barrosi* Philippi, 1887 (Nielsen & Valdovinos, 2008: 203).
- arcaiformis*, *Nucula* – Philippi, 1887a: 193–194 [1887b: 187], pl. 41, fig. 18. Hualpen, Chile; Cretaceous. Syntype, SGO.PI.333 (n = 1, labeled as "holotipo"). *Nomen dubium* (Villarroel & Stuardo, 1998: 171: "probablemente una *Barbatia*").
- barrosi*, *Nucula* – Philippi, 1887a: 198 [1887b: 191], pl. 41, fig. 14. Mouth of Río Rapel, Chile?; Diego Barros; Tertiary. Syntypes,



- SGO.PI.306 (n = 1 valve, labeled as “lectotipo”); SGO.PI.5046 (n = 1 valve, labeled as “paralectotipo”). The Pliocene *Nucula* (*Leionucula*) *barrosi* Philippi, 1887 (Frassinetti, 1997: 58, 68–69, pl. 1, figs. 1, 2), although Villarroel & Stuardo (1998: 171) thought that this was a *nomen dubium* (“un venérado?”).
- compressa*, *Nucula* – Philippi, 1847-I: 54, pl. 8, fig. 6, *non* J. De. C. Sowerby, 1837. Wilhelmshöhe, Hessen, Germany; [Late Oligocene]; Landgrebe in Cassel. Synonym of *Nucula schmidtii* Glibert, 1955 (Rust, 1999: 27; R. Janssen, pers. comm., April 2013). Type material lost (R. Janssen, pers. comm., April 2013).
- compressiuscula*, *Nucula* – Philippi, 1899: 61, pl. 26, fig. 11. Portezuelo del Tinguiririca, Chile; Jurassic. *Nucula compressiuscula* Philippi, 1899; Upper Jurassic and Lower Cretaceous (Villarroel & Stuardo, 1998: 163).
- cornuta*, *Nucula* “?” – Philippi, 1887a: 193 [1887b: 186–187], pl. 41, fig. 20. “Tumbez”, Chile; Cretaceous. *Nomen dubium* (Villarroel & Stuardo, 1998: 171).
- cuspidata*, *Nucula* – Philippi, 1844g: 47, pl. 15, fig. 8, 8a. Lamati, Calabria, Italy; Pleistocene. *Thestyloda cuspidata* (Philippi, 1844) (Di Geronimo & La Perna, 1997: 407–408, pl. 6, figs. 1–4, 9–11).
- dechenii*, *Nucula* – Philippi, 1847-I: 52–53, pl. 8, fig. 7. Westeregeln, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene; Berlin Museum. *Nucula dechenii* Philippi, 1847 (R. Janssen, pers. comm., April 2013). PHB MB M \_\_\_\_ (K) 75, syntypes (9 valves + fragments) (Westeregeln).
- decipiens*, *Nucula* – Philippi, 1844g: 48, 300, pl. 15, fig. 15, 15a. Lamati, Calabria, Italy; fossil. Sabelli et al. (1990: 274) erroneously listed this as a junior synonym of *Ennucula aegensis* (Forbes, 1844), which was actually published later in 1844. *Ennucula decipiens* (Philippi, 1844), Pleistocene to Recent (La Perna, 2007b: 117, pl. 8, figs. 7–11).
- delaiguei*, *Nucula* – Philippi, 1899: 61, pl. 28, fig. 8. Cañon del Río Negro, Argentina; Alberto Delaigue; Plagemann coll.; [Mesozoic?].
- discors*, *Nucula* – Philippi, 1887a: 196 [1887b: 189], pl. 41, fig. 23. Arauco Province, Chile; Francisco J. Ovalle; Tertiary. Syntype, SGO.PI.305 (n = 1, labeled as “holotipo”). *Nucula discors* Philippi, 1887 (Villarroel & Stuardo, 1998: 163).
- glabra*, *Nucula* – Philippi, 1844g: 47, 300, pl. 15, fig. 6. Calabria, Italy; fossil.
- hualpensis*, *Nucula* – Philippi, 1887a: 194 [1887b: 187], pl. 56, fig. 3. Hualpen, Chile; Cretaceous. Syntypes, SGO.PI.329 (n = 2 valves). *Nomen dubium* (Villarroel & Stuardo, 1998: 171; “Podría ser Malletiidae”).
- lauta*, *Nucula* – Philippi, 1887a: 196 [1887b: 189], pl. 31, fig. 2. Lebu, Chile; Tertiary. Syntype, SGO.PI.327 (n = 1 valve, labeled as “holotipo”). *Nomen dubium* (Villarroel & Stuardo, 1998: 171).
- lebuensis*, *Nucula* – Philippi, 1887a: 198 [1887b: 191], pl. 41, fig. 15. Lebu, Chile; Tertiary. Syntypes, SGO.PI.319 (n = 1), SGO.PI.328 (n = 1 valve), SGO.PI.5043 (n = 1), SGO.PI.5044 (n = 1), SGO.PI.5045 (n = 1). *Nucula* (*Leionucula*) *lebuensis* Philippi, 1887; Miocene (Frassinetti, 2004: 73, 2006: 63). Nielsen & Valdovinos (2008: 203) determined that the records attributed to this species by Villarroel & Stuardo (1998: 165–166, figs. 138–139) were actually *Ennucula grayi* (d’Orbigny, 1846).
- limosa*, *Nucula* – Philippi, 1845g: 75–76. Hudson Bay, Canada. *Nomen dubium* (Huber, 2010: 536).
- lunularis*, *Nucula* – Philippi, 1899: 62, unfigured. Portezuelo del Tinguiririca, Chile; Jurassic. *Nomen dubium*, possibly referable to the Nuculanidae (Villarroel & Stuardo, 1998: 171).
- nogalis*, *Nucula* – Philippi, 1899: 61–62, pl. 28, fig. 9. Nogales, N. of Agua de los Pajaritos, Chile; Mesozoic. *Ennucula nogalis* (Philippi, 1899); Neocomian, Cretaceous (Villarroel & Stuardo, 1998: 164).
- ovallei*, *Nucula* – Philippi, 1887a: 193 [1887b: 186], pl. 41, fig. 12. “Tumbez”, Chile; Francisco J. Ovalle; Cretaceous. *Nucula ovallei* Philippi, 1887 (Villarroel & Stuardo, 1998: 164).
- patagonica*, *Nucula* – Philippi, 1887a: 198 [1887b: 191], pl. 41, fig. 8. Santa Cruz, Chile; Ramón Vidal Gormáz; Tertiary. Syntype, SGO.PI.314 (n = 1, Santa Cruz, labeled as “holotipo”). Del Río & Camacho (1996: 938) determined that Philippi’s species was “an unrecognizable species” based on an internal mold, and because several species of Nuculidae are now known from that locality, they introduced *Iheringinuclula crassirugata* as “a new name for the material found at the mouth of the Santa Cruz River” (Eocene, Patagonia, Argentina). Villarroel & Stuardo (1998: 163–164) and Ihering (1907: 226) had treated Philippi’s species as a valid species of *Nucula*.
- pellucida*, *Nucula* – Philippi, 1844g: 48, 300, pl. 15, fig. 9, 9a. Monasterace, Calabria, Sicily, Italy; fossil.



*polii*, *Nucula* – Philippi, 1836a: viii, 63–64, pl. 5, fig. 10. Sicily, Italy: living and fossil. Synonym of *Nucula sulcata* Bronn, 1831 (Sabelli et al., 1990: 273).

*pusilla*, *Nucula* – Philippi, 1899: 61, pl. 26, fig. 12. Portezuelo del Tinguiririca, Chile; Mesozoic. *Nucula pusilla* Philippi, 1899 (Villarroel & Stuardo, 1998: 164).

*quisuilla*, *Nucula* “?” – Philippi, 1899: 60, pl. 26, fig. 9. Portezuelo del Tinguiririca, Chile; Mesozoic. *Nomen dubium* (Villarroel & Stuardo, 1998: 171).

*subcarinata*, *Nucula* – Philippi, 1899: 59, pl. 26, fig. 6. Portezuelo del Tinguiririca, Chile; Mesozoic. *Nomen dubium* (Villarroel & Stuardo, 1998: 171).

*subglobosa*, *Nucula* – Philippi, 1847-I: 53, pl. 8, fig. 5. Dömitz im Mecklenbergischen (NE of Dannenberg, state of Mecklenburg-Vorpommern), Germany; Fr. Hoffmann; Middle Miocene. Type material in PHB MB M \_\_\_\_ (R. Janssen, in litt., 9 Feb. 2016).

*subradiata*, *Nucula* – Philippi, 1899: 59, pl. 26, fig. 5. Portezuelo del Tinguiririca, Chile; Mesozoic. *Nomen dubium* (Villarroel & Stuardo, 1998: 171).

*tinguiriricana*, *Nucula* “?” – Philippi, 1899: 60, pl. 26, fig. 7. Portezuelo del Tinguiririca, Chile; Mesozoic. *Nomen dubium* (Villarroel & Stuardo, 1998: 171).

*triangula*, *Nucula* – Philippi, 1899: 60–61, pl. 26, fig. 10. Portezuelo del Tinguiririca, Chile; Mesozoic. *Nomen dubium* (Villarroel & Stuardo, 1998: 171).

*valdiviana*, *Nucula* – Philippi, 1887a: 197 [1887b: 190–191], pl. 41, fig. 22. Llancahue (Wilhelm Frick) & mouth of Río Rapel, Chile; Tertiary. Syntypes, SGO.PI.320 (n = 1, Llancahue); SGO.PI.335 (n = 1 valve, Río Rapel). Nielsen & Valdovinos (2008: 203) determined that the records attributed to this species by Villarroel & Stuardo (1998: 166, figs. 134–137) were actually *Ennucula grayi* (d’Orbigny, 1846).

*vicentina*, *Nucula* – Philippi, 1887a: 192–193 [1887b: 186], pl. 57, fig. 5. San Vicente, Chile; Cretaceous. SGO.PI.332 is erroneously labeled as the “holotipo” but it is from Hualpen, which is not the type locality.

#### Solemyidae

*antarctica*, *Solenomya* – Philippi, 1887a: 186 [1887b: 179], pl. 42, fig. 5. Mouth of Río Rapel, Chile; Tertiary. *Solenomya antarctica* Philippi, 1887 (Villarroel & Stuardo, 1998:

169), or *Solemya (Petrasma) antarctica* (Philippi, 1887) (Bernard, 1983: 9).

#### Nuculanidae

*Monopleura* – Philippi, 1887a: 198–199 [1887b: 191–192], *non* Matheron, 1842 [Bivalvia]. Type species (M): *Monopleura ambigua* Philippi, 1887. Possibly Nuculanidae or Yoldiidae; as a junior synonym of *Nuculana* Link, 1807 (Puri, 1969: N235).

*ambigua*, *Monopleura* – Philippi, 1887a: 199 [1887b: 192], pl. 37, fig. 12. Tumbez Peninsula near San Vicente, Chile; Tertiary. SGO.PI.633 (n = 1 valve, labeled as “holotipo”). Wilckens (1904: 226–227, pl. 19, figs. 1, 2) listed this under “*Naiadina* Munier-Chalmas,” as “*Naiadina* “?” *ambigua*” (Philippi, 1887), which is in error, as *Naiadina* Munier-Chalmas, 1864 is in the Malleiidae (Pteriomorphia), and Philippi’s illustration of his species does not correspond to the Malleiidae.

*analís*, *Nucula* – Philippi, 1851c: 87. China; Largilliert. Synonym of *Saccula mauritiana* (G. B. Sowerby I, 1833) (Huber, 2010: 97, 531).

*chiloensis*, *Nucula* – Philippi, 1858a: 125. Calbuco, Chile; Germain. Not mentioned by Villarroel & Stuardo (1998) or Letelier et al. (2003). Probably a *Saccula* (P. Valentich-Scott, in litt., 21 Mar. 2015).

*commutata*, *Nucula* – Philippi, 1844n: 101; Philippi, 1845z: 448. Mediterranean, living and fossil. *Saccula commutata* (Philippi, 1844) (Aartsen & Carrozza, 1987; Sabelli et al., 1990: 275; Giribet & Peñas, 1997: 56 [18], as *Nuculana*; Huber, 2010: 96; Janssen & Krylova, 2014: 49). This is the senior available name for the type species (OD) of *Ledina* Sacco, 1898 (Dec.), *non* *Ledina* Dall, 1898 (Nov.), *Arca fragilis* Deshayes, 1848, ex Chemnitz ms. Sacco’s genus was renamed *Saccula* Woodring, 1925. Beu (2006: 176) discussed the nomenclature of Philippi’s *commutata* (including the possible but unused senior synonym *Lembulus deltoideus* Risso, 1826) [Nuculanidae].

*darwiní*, *Nucula* – Philippi, 1887a: 195 [1887b: 188], pl. 41, fig. 17. Lebu, Chile; Tertiary. *Propeleda darwiní* (Philippi, 1887) (Villarroel & Stuardo, 1998: 167).

*dorbignyí*, *Nucula* – Philippi, 1887a: 195 [1887b: 188], pl. 41, fig. 10. Lebu, Chile; Tertiary. *Propeleda dorbignyí* (Philippi, 1887) (Villarroel & Stuardo, 1998: 167–168).



*errazurizi*, *Nucula* – Philippi, 1887a: 196 [1887b: 189], pl. 41, fig. 11a–c. Lebu, Chile; Maximiano Errazuriz; Tertiary. Syntype, SGO.PI.334 (n = 1, labeled as “holotipo”). *Nuculana errazurizi* (Philippi, 1887) (Villarroel & Stuardo, 1998: 166).

*largillierti*, *Nucula* – Philippi, 1851c: 87–88. Gabon; Largilliert. Synonym of *Lembulus bicuspidatus* (Gould, 1845) (Huber, 2015: Chapter 5 on CD).

*medinae*, *Nucula* – Philippi, 1887a: 195 [1887b: 188–189], pl. 41, fig. 24. Mouth of Río Rapel, Chile; Tertiary. Syntype, SGO.PI.332 (n = 1 valve, labeled as “holotipo”). *Propeleda medinae* (Philippi, 1887); Eocene-Miocene (Villarroel & Stuardo, 1998: 167).

*oxyrrhyncha*, *Nucula* – Philippi, 1887a: 197 [1887b: 190], pl. 41, fig. 21. Lota (Volckmann), Lebu & Navidad, Chile; Tertiary. Syntype, SGO.PI.315 (n = 1 valve, Lota); SGO.PI.317 (n = 1 valve, Lebu); SGO.PI.330 (n = 1 valve, Navidad). “*Leda*” [= *Nuculana*] *oxyrrhyncha* (Philippi, 1887); Miocene (Tavera, 1979: 85). *Nuculana oxyrrhyncha* (Philippi, 1887) (Villarroel & Stuardo, 1998: 166–167).

*sanctaemariae*, *Nucula* – Philippi, 1887a: 195 [1887b: 188], pl. 41, fig. 2, as “*N. sanctae mariae*”. Isla Santa Maria, Chile; MacSporran; Tertiary. Holotype, SGO.PI.307 (n = 1 valve). Possibly referable to the Nuculanidae (Villarroel & Stuardo, 1998: 171, as a “*nomen dubium*”); or *Nuculana* (*Sacella*) *sanctamariae* (Philippi, 1887) (D. Frassinetti, note in SGO.PI collection).

#### Malletiidae

*dilatatae*, *Nucula* – Philippi, 1844g: 47–48, 300, as “*N. dilitata*”, pl. 15, fig. 7. Lamati, Calabria, Italy; fossil. *Malletia dilatatae* (Philippi, 1844), which may also occur in the western Atlantic (Tunnell et al., 2010: 304), although Huber (2010: 539) considered western Atlantic material to probably represent an undescribed species.

*pencana*, *Nucula* – Philippi, 1887a: 192 [1887b: 185], pl. 41, fig. 5. Hualpen, Chile; Wenceslao Diaz; Cretaceous. Syntype, SGO.PI.325 (n = 1 valve, labeled as “lectotipo”); SGO.PI.4805–4808 (n = 4 valves, labeled as “paralectotipo”). *Malletia* (*Neilo*) *pencana* (Philippi, 1887) (Wilckens, 1904: 230, pl. 19, fig. 6; Wetzel, 1930: 75; Villarroel & Stuardo, 1998: 169); or *Neilo* (*N.*) *pencana* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1986: 166–167, pl. 1, figs. 12–14).

*pusio*, *Nucula* – Philippi, 1844g: 47, 300, pl. 15, fig. 5, 5a. Bianco & Lamati, Calabria, Italy; Pleistocene. Type species (M) of *Saturnia* Seguenza, 1877, *non* Schrank, 1802 [Lepidoptera]. *Pseudoneilonella* Laghi, 1986, *nom. nov. pro Saturnia* Seguenza. This species has been variously interpreted, in part because of the missing type material, but also because the arrangement of protobranch genera is far from settled. It was listed as *Neilonella pusio* (Philippi, 1844) by Sabelli et al. (1990: 275). Allen & Sanders (1996: 103) stated that Philippi’s species is “not a neilonellid, but a ledellid,” thus *Ledella pusio* [Nuculanidae], and this was recently followed by Paone Viegas et al. (2014: 186). However, based on study of Italian fossil material, La Perna (2007a: 199–201, fig. 4), treated this as *Pseudoneilonella pusio* (Philippi, 1844), which we think is the best researched placement. Huber (2010: 541) listed it as a *nomen dubium*, apparently unaware of La Perna’s (2007a) paper; Huber (2015: 362) discussed but did not accept La Perna’s conclusions. Some authors have placed *Neilo* and *Pseudoneilonella* in the Neilonellidae, but Huber (2010: 103–104, 538–539) made a convincing argument for synonymizing the Neilonellidae with the Malletiidae.

*quiriquinae*, *Nucula* – Philippi, 1887a: 192 [1887b: 185], pl. 41, fig. 6. Isla Quiriquina, Chile; Cretaceous. Syntype, SGO.PI.338 (n = 1 valve, labeled as “holotipo”). *Nomen dubium* (Villarroel & Stuardo, 1998: 171), or *Neilo* (*Neilo*) *quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1986: 167, pl. 1, figs. 15–16).

*volckmanni*, *Nucula* – Philippi, 1887a: 194–195 [1887b: 188], pl. 41, fig. 9. Tubul (Volckmann) & Lebu, Chile; Tertiary. Syntypes, SGO.PI.331 (n = 1, Tubul, labeled as “lectotipo”), SGO.PI.5039–5042 (n = 1 specimen + 3 valves, Tubul, labeled as “paralectotipo”); SGO.PI.326 (n = 1, Lebu). *Malletia volckmanni* (Philippi, 1887); Miocene (Tavera, 1979: 82–83, pl. 14, fig. 30; Villarroel & Stuardo, 1998: 169–170, figs. 144–145).

#### Yoldiidae

*excisa*, *Nucula* – Philippi, 1844g: 46, 300, pl. 15, fig. 4, 4c. Monterosso, Lamato, Stilo & Cotrone, Calabria, Italy; Pleistocene. *Bathyspinula excisa* (Philippi, 1844) (Di Geronimo & La Perna, 1997: 412, pl. 7 = p. 409, figs. 7–9). Dalsum (1959: 29–30) deter-



mined that *Leda excisa sensu* Nyst (1868), *non* Philippi, was referable to *Yoldia glaberrima* (Münster, 1837); *Malletia excisa sensu* Jeffreys (1876), *non* Philippi, is *Bathyspinula subexcisa* (Dautzenberg & Fischer, 1897) (Janssen & Krylova, 2014: 46).

*tenuis*, *Nucula* – Philippi, 1836a: viii, 65–66, pl. 5, fig. 9a, 9b, *non* Montagu, 1808. Palermo, Sicily, Italy; fossil. Possible syntypes, PHB MB M.550 (K) 77 (n = 3) (missing in 2013). *Nucula philippiana* Nyst, 1845, was proposed as a replacement name. *Yoldiella philippiana* (Nyst, 1845) (Sabelli et al., 1990: 276; Higo et al., 1999: 409; Kantor & Sysoev, 2005: 314; Killeen & Turner, 2009: 754–755, fig. 21; Janssen & Krylova, 2014: 53).

### Mytilidae

*andina*, *Modiola* – Philippi, 1899: 47, pl. 24, figs. 3, 12, var. Baños del Toro, Chile; Vicente Magallanes. Aberhan (1994: 47) tentatively synonymized this with *Modiolus baylei* (Philippi, 1899), a Jurassic species.

*angustata*, *Modiola barbata* “Lamarck” var. – Philippi, 1836a: 70 (as “var.  $\beta$  angustata”). Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1890: 154, pl. 27, fig. 7) as *Modiolus barbata* var. *angustata*, and by Lamy (1936: 262–266) as *Modiolus barbatus* var. *angustata*.

*angustatus*, *Mytilus galloprovincialis* Lamarck var. – Philippi, 1836a: 72 (as “var.  $\beta$  angustatus”). Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1890: 140) and Lamy (1936: 95, 98) as *Mytilus galloprovincialis* var. *angustata*.

*antarctica*, *Modiola* – Philippi, 1868: 224. Strait of Magellan, Chile; William Acton. Lamy (1936: 266) stated that this resembles a juvenile *Modiolus barbatus* (Linnaeus, 1758); or as *Philobrya antarctica* (Philippi, 1868) (Bernard, 1983: 16), which would place it in the Philobryidae.

*antillarum*, *Modiola* (*Lithophagus*) – Philippi, 1847r: 116; 1847v: 20 [6], pl. 2, fig. 4. St. Thomas, Virgin Islands; Hornbeck. Regarded as a synonym of *Lithophaga caribaea* (Philippi, 1847) (Huber, 2010: 551), or as a synonym of the widespread *Lithophaga* (*Lithophaga*) *teres* (Philippi, 1846) (Kleemann & Maestrati, 2012: 75–78). “Reversal of Precedence” invoked by Mikkelsen & Bieler (2007: 413–414; Bieler, 2010) to conserve the Caribbean *L. nigra* (d’Orbigny, 1853), which they regarded

as the same species. Syntypes, MNHNS 236 (n = 1v) (44.2 mm x 12.6 mm); SMF 315184 (n = 1) (37.1 mm x 12.1 mm); ZMB 117920 (4 valves; Hornbeck, St. Thomas) (47.6 mm x 14.3 mm; 42.3 mm x 12.4 mm). Kleemann & Maestrati (2012: 75) incorrectly stated “type material probably lost”.

*appendiculata*, *Modiola* – Philippi, 1846y: 150 [4], pl. 1, fig. 4. Cuba. The western Atlantic *Lithophaga* (*Leiosolenus*) *appendiculatus* (Philippi, 1846) (Kleeman, 2009: 23–24; Huber, 2010: 120, 551). MNHNS 50675 (largest specimen, figured by Philippi), selected as lectotype (Kleeman, 2009: 23, fig. 1); paralectotypes, MNHNS 50675 (n = 3). Reversal of Precedence invoked by Bieler (2010) to conserve the Caribbean *L. bisulcatus* (d’Orbigny, 1853).

*baylei*, *Modiola* – Philippi, 1899: 48, pl. 24, fig. 8. *Modiolus baylei* (Philippi, 1899), Jurassic (Damborenea, 1987a: 91–92, pl. 4, figs. 2–5; Aberhan, 1994: 47–48, pl. 26, figs. 1–4).

*californiensis*, *Modiola* – Philippi, 1847r: 113, ex Eschscholtz ms. California; Eschscholtz. *Adula californiensis* (Philippi, 1847) (Coan et al., 2000: 176–178, pl. 28; Huber, 2010: 121).

*caperatus*, *Lithophagus* – Philippi, 1849r: 25–26. Liewkiew Island [Ryukyu Island, Japan]; Cécille via Largilliert. Synonym of the Indo-Pacific *Lithophaga corrugata* (Philippi, 1846) (Kleemann & Maestrati, 2012: 74–75), treated as a senior synonym of the western Atlantic *L. antillarum* d’Orbigny, 1853. However, Huber (2010: 119, 551) considered *L. corrugata* to be a distinct western Pacific species; Huber (2015: 365) stated that “Kleeman et al.’s ‘circumtropical’ distribution is false”, and the “broad *corrugata*-synonymy of Kleeman et al. (2012: 74) is unsubstantiated.”

*caribaea*, *Modiola* (*Lithophagus*) – Philippi, 1847r: 116–117; 1847v: 21 [7], pl. 2, fig. 6. Antilles; Gruner. Treated as a distinct Caribbean species by Huber (2010: 119, 551; 2015: 365); regarded as a synonym of the widespread *Lithophaga* (*Lithophaga*) *teres* (Philippi, 1846) (Kleemann & Maestrati, 2012: 75–78). “Reversal of Precedence” invoked by Mikkelsen & Bieler (2007: 413–414; 2010) with respect to the Caribbean *L. nigra* (d’Orbigny, 1853), which they regarded as the same species. Type material probably lost (Kleemann & Maestrati, 2012).

*cecilli*, *Modiola* – Philippi, 1847r: 114. China; Cécille; Largilliert collection. Syntypes, Muséum de Rouen 143001005 (63.2 mm x 32.7 mm); MNHNS 50655 (n = 1 valve, broken) (58.4 mm x 31.1 mm). The western



- Pacific *Modiolus cecilli* (Philippi, 1847) (Lamy, 1936: 292–293; Huber, 2010: 122, 554, as *M. "cecilli"*).
- contracta*, *Modiola* – Philippi, 1899: 47, pl. 24, fig. 4. Peñon, Atacama, Chile; Arit. Martinez; [Mesozoic].
- coquandi*, *Modiola* – Philippi, 1899: 47, pl. 24, fig. 5. Baños del Toro, Chile; Vicente Magallanes; [Mesozoic].
- coquimbana*, *Modiola* – Philippi, 1887a: 203–204 [1887b: 196–197], pl. 44, figs. 1, 7, “var.”. Coquimbo, Chile; Tertiary. Syntypes, SGO. Pl.492 (n = 1, labeled as “lectotipo”); SGO. Pl.4818 (n = 1, labeled as “paralectotipo”).
- corrugata*, *Modiola* – Philippi, 1846y: 148 [1], pl. 1, fig. 1; 1847v: 21 [7]. Locality unknown; West Indies (Philippi, 1847v). *Lithophaga corrugata* (Philippi, 1846) (Wilson, 1979: 447–449; Huber, 2010: 119, 551; Kleemann & Maestrati, 2012: 74–75). However, Huber (2010: 119, 551; 2015: 365) concluded that this species was limited to the Caribbean, contrary to Wilson and Kleemann & Maestrati, who extended the distribution of this species to the Indo-Pacific. Reversal of Precedence invoked by Bieler (2010) to conserve the Caribbean *L. antillarum* (d’Orbigny, 1853).
- crispata*, *Modiola* (*Lithophagus*) – Philippi, 1849i: 155. Bourbon; Largilliert. Genus uncertain (Kleemann, 1983: 7); possible senior synonym of *Leiosolenus malaccanus* (Reeve, 1857) (Huber, 2010: 120, 552).
- dactyloides*, *Mytilus* – Philippi, 1860a: viii, 177; 1860b: 159, 174. Unjustified emendation of *Modiolus dactyliformis* Hupé in Gay, 1854, as noted by Lamy (1937: 311).
- dilatata*, *Modiola barbata* “Lamarck” var. – Philippi, 1836a: 70 (as “var.  $\alpha$  dilatata”). Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1890: 154, pl. 27, fig. 8–9) as *Modiolus barbata* var. *dilatata*, and by Lamy (1936: 262–266) as *Modiolus barbatus* var. *dilatata*.
- dilatata*, *Mytilus minimus* Poli var. – Philippi, 1836a: 73 (as “var.  $\alpha$  dilatata”). Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1890: 148, pl. 26, fig. 4–5) as *Mytilus minimus* var. *dilatata*, and by Lamy (1936: 233–234) as *Brachidontes* (*Mytilaster*) *minimus* var. *dilatata*.
- dilatatus*, *Mytilus galloprovincialis* Lamarck var. – Philippi, 1836a: 72 (as “var.  $\alpha$  dilatatus”). Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1890: 140, pl. 25, fig. 6–7) and Lamy (1936: 94–95, 98) as *Mytilus galloprovincialis* var. *dilatata*.
- divaricata*, *Modiola* – Philippi, 1847r: 115–116; 1847v: 21–22 [7–8], pl. 2, fig. 8, *non* d’Orbigny, 1853. Antilles. MNHNS 5237 (n = 2 valves) (labeled as “holotipo” but from Panama, which is not the type locality). Synonym of the widespread *Gregariella coralliophaga* (Gmelin, 1791) (Higo et al., 1999: 417).
- exaratus*, *Mytilus* – Philippi, 1847r: 119–120. Locality unknown. Syntype, MNHNS 197 (n = 1, “Chile”) (11.9 mm x 6.8 mm). Synonym of *Brachidontes purpuratus* (Lamarck, 1819) (Bernard, 1983: 18).
- exilis*, *Mytilus* – Philippi, 1847r: 120. Chile & Peru; Kröyer. Syntypes, MNHNS (n = 3) (largest, 8.4 mm x 4.4 mm). Synonym of *Brachidontes purpuratus* (Lamarck, 1819) (Bernard, 1983: 18).
- ferruginea*, *Modiola* (*Lithophagus*) – Philippi, 1847r: 118; 1847v: 19–20 [5–6], pl. 2, fig. 3. Locality unknown. Probable syntypes, MNHNS 50346 (n = 2) (93.1 mm x 27.3 mm; 83.5 mm x 27.6 mm). Synonym of the western Atlantic *Lithophaga antillarum* d’Orbigny, 1853 (Kleemann, 1983: 10; Huber, 2010: 551). Not mentioned by Mikkelsen & Bieler (2007: 413–414), although they conserved d’Orbigny’s taxon by Reversal of Precedence from two other pre-1853 Philippi taxa.
- foncki*, *Modiola* – Philippi, 1887a: 204 [1887b: 197], pl. 43, fig. 1. Lebu, Chile; Tertiary. Holotype, SGO.Pl.446 (n = 1 valve).
- gracilis*, *Modiola* (*Lithophagus*) – Philippi, 1847r: 117–118; 1847v: 19 [5], pl. 2, fig. 1. China. Regarded as a synonym of the widespread *Lithophaga* (*Lithophaga*) *teres* (Philippi, 1846) (Wilson, 1979: 439; Lamprell & Healey, 1998: 92–93, fig. 214; Kleemann & Maestrati, 2012: 75–78). MNHNS 50338, holotype (Kleemann, 1984: 210, fig. 23).
- grandis*, *Modiola* – Philippi, 1844g: 51, 300, pl. 15, fig. 13. Calabria, Italy; fossil. Synonym of *Modiolus modiolus* (Linnaeus, 1758) (Bernard, 1983: 19–20; Kantor & Sysoev, 2005: 316).
- gruneri*, *Modiola* (*Lithophagus*) – Philippi, 1851c: 85–86. Locality unknown; Gruner coll. The northeastern Pacific *Adula gruneri* (Philippi, 1851) (Kleemann, 1983: 11; Coan et al., 2000: 178–179, pl. 28). Ruhoff (1980: 300) listed “*Lithodomus gruneri*” as being by “Philippi, in Reeve” (i.e., Reeve, 1857b, pl. 3, fig. 12), but Philippi had already described this species in 1851.
- incurvata*, *Modiola* – Philippi, 1836a: viii, 72, pl. 4, fig. 20; 1844g: 52. Piazza, Sicily, Italy; fossil [Late Pliocene – Early Pleistocene].



- incurvata*, *Mytilus minimus* Poli var. – Philippi, 1836a: 73 (as “var.  $\gamma$  incurvata”). Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1890: 148) as *Mytilus minimus* var. *incurvata*, and by Lamy (1936: 233–234) as *Brachidontes (Mytilaster) minimus* var. *incurvata*.
- laeviuscula*, *Modiola* – Philippi, 1887a: 204 [1887b: 197], pl. 44, fig. 5. Lebu, Chile; Francisco J. Ovalle; Tertiary.
- legumen*, *Modiola* – Philippi, 1851c: 86. Locality unknown. Status uncertain; type material not located (Huber, 2010: 556).
- lepida*, *Modiola* – Philippi, 1893b: 12, pl. 2, fig. 3. Argentina; Tertiary. *Brachidontes (B.) rodriguezi* subsp. *lepida* (Philippi, 1893); Miocene (del Río, 1991: 45, pl. 2, fig. 6; del Río & Martínez, 1998: 53, pl. 16, fig. 11, pl. 17, fig. 9).
- lepidus*, *Mytilus* – Philippi, 1899: 46, pl. 24, fig. 2. Doña Ana [Coquimbo], Chile. Syntype, SGO.PI.930 (n = 1).
- lotensis*, *Mytilus* – Philippi, 1887a: 201 [1887b: 194], pl. 43, fig. 3. Lota, Chile; Volckmann; Tertiary. Holotype, SGO.PI.448 (n = 1 valve). Lamy (1936: 150–151) stated that this was probably just a variety of *Mytilus magellanicus* Lamarck, 1819.
- malayana*, *Modiola (Lithophagus)* – Philippi, 1847r: 117; 1847v: 20 [6], pl. 2, fig. 4. China. Regarded as a synonym of the widespread *Lithophaga (Lithophaga) teres* (Philippi, 1846) (Wilson, 1979: 439; Higo et al., 1999: 420; Kleemann & Maestrati, 2012: 75–78). Type material probably lost (Kleemann & Maestrati, 2012).
- menkeanus*, *Mytilus* – Philippi, 1847r: 118–119. Australia; Preiss. Synonym of *Brachidontes erosus* (Lamarck, 1819) (Lamy, 1936: 166–167; Lamprell & Healey, 1998: 78–79, fig. 157). Ruhoff (1980: 369) listed “*Mytilus menkeanus*” as being by “Philippi, in Reeve” (i.e., Reeve, 1857a, pl. 7, fig. 26), but Philippi had already described this species in 1847.
- mucronata*, *Modiola* – Philippi, 1846y: 150 [4], pl. 1, fig. 8. Java. Syntype, MNHNS 50636 (n = 14 valves). The Indo-Pacific *Lithophaga mucronata* (Philippi, 1846) (Kleemann, 1983: 16; Kleeman & Hoeksema, 2002: 19–20, fig. 11; Qi, 2004: 233, pl. 123D; Huber, 2010: 121; Severns, 2011: 436–437, fig. 5; Kleemann & Maestrati, 2012: 88–90, figs. 8A–C, 9).
- nannus*, *Mytilus* – Philippi, 1899: 46, pl. 24, fig. 10. Portezuelo del Tinguiririca, Chile; Frid. Albert; [Mesozoic].
- nasuta*, *Modiola* – Philippi, 1846y: 149 [3], pl. 1, fig. 2. Indo-Pacific. The Indo-Pacific *Lithophaga (Leiosolenus) nasuta* (Philippi, 1846) (Wilson, 1979: 457–461, pl. 17, fig. 2; Lamprell & Healey, 1998: 92–93, fig. 217; Higo et al., 1999: 421; Kleemann & Maestrati, 2012: 90–92, fig. 10A–C). MNHNS 50391, syntype, probably lost; MNNHS 50344, lectotype (Kleemann & Maestrati, 2012).
- navidadis*, *Mytilus* – Philippi, 1887a: 201 [1887b: 194], pl. 43, fig. 4. Navidad, Chile; Tertiary. *Mytilus navidadis* Philippi, 1887; Miocene (Tavera, 1979: 84, pl. 15, fig. 34).
- obesa*, *Modiola (Lithophagus)* – Philippi, 1847r: 118; 1847v: 19 [5], pl. 2, fig. 2. China “?”. Syntype, MNHNS 50341 (n = 1) (42 mm x 16.5 mm) (rediscovered March 2013). Neotype, AMS C60407 (designated by Wilson, 1979: 474, pl. 17, fig. 1; this is the holotype of *L. obesa suspecta* Iredale, 1939, a junior synonym). ICZN Code Article 75.8 (1999) applies, and the syntype takes precedence over the neotype. The Indo-Pacific *Lithophaga (Leiosolenus) obesa* (Philippi, 1847) (Wilson, 1979: 474–476, pl. 17, fig. 1; Kleeman, 1983: 17; Lamprell & Healey, 1998: 94–95, fig. 222; Higo et al., 1999: 420; Okutani, 2000: 876–877, fig. 77; Qi, 2004: 233, pl. 123-I; Kleemann & Maestrati, 2012: 90–92, fig. 11A–C).
- obesus*, *Mytilus* – Philippi, 1887a: 202–203 [1887b: 195–196], pl. 44, fig. 9. Living & Cahuil, Chile; Quaternary. SGO.PI.199 is labeled as “tipo”, but it was collected in 1894, subsequent to the 1887 description.
- phaseolina*, *Modiola* – Philippi, 1844g: 51–52, 300, pl. 15, fig. 14. Calabria, Italy; fossil. The eastern Atlantic *Modiolula phaseolina* (Philippi, 1844) (Janssen, 1972: 15–16, pl. 2, fig. 3; Sabelli et al., 1990: 285; Giribet & Peñas, 1997: 57 [19]; Kantor & Sysoev, 2005: 316; Huber, 2010: 125; Janssen & Krylova, 2014: 75) and type species (OD) of the genus *Modiolula* Sacco, 1898. Also known from New Zealand (Beu, 2004: 144–146, fig. 8).
- plagemanni*, *Modiola* – Philippi, 1899: 48, pl. 24, fig. 9. Primon de las Promasas (Nogales), Anconcagua, Chile; Alb. Plagemann.
- platensis*, *Lithophagus* – Philippi, 1893b: 12, pl. 3, fig. 3. Argentina; Tertiary. *Lithophaga platensis* (Philippi, 1893), Miocene (Ihering, 1907: 380; del Río & Martínez, 1998: 53–54). Turner & Boss (1962: 102, 104) incorrectly stated that this species was originally described in *Lithodomus*.



- platensis*, *Modiola* – Philippi, 1893b: 11–12, pl. 2, fig. 2. Argentina; Tertiary. *Modiolus platensis* (Philippi, 1893), Miocene (del Río & Martínez, 1998: 53, pl. 17, fig. 10).
- poliana*, *Modiola* – Philippi, 1844n: 101–102. Mediterranean, living and fossil. Synonym of *Musculus subpictus* (Cantraine, 1835) (Sabelli et al., 1990: 283).
- promaucana*, *Modiola* – Philippi, 1887a: 204 [1887b: 197], pl. 44, fig. 3. Navidad, Chile; Tertiary [Miocene].
- promaucanus*, *Mytilus* – Philippi, 1887a: 201–202 [1887b: 194–195], pl. 44, fig. 8. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.445 (n = 1 valve).
- prunum*, *Modiola* – Philippi, 1899: 48, pl. 24, fig. 13. Andibus Chillanensibus; Frid. Puga; [Mesozoic].
- pullus*, *Mytilus* – Philippi, 1899: 46, pl. 24, fig. 11. Locality not given, Chile; Volckmann; [Mesozoic].
- pusilla*, *Modiola* – Philippi, 1899: 47, pl. 24, fig. 6. Portezuelo del Tinguiririca, Chile; Frid. Albert; [Mesozoic].
- pygmaea*, *Modiola* – Philippi, 1841f: 15; 1844z4: 15, [86], pl. 2, fig. 14; Philippi, 1844g: 214. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Modiolula pygmaea* (Philippi, 1841) (Janssen, 1979b: 43–44; Rust, 1999: 31, both dated the species from 1843). Type material lost (R. Janssen, pers. comm., April 2013).
- ramosus*, *Mytilus* – Philippi, 1887a: 200–201 [1887b: 193–194], pl. 43, fig. 2. Lebu, Chile; Tertiary. Holotype, SGO.PI.442 (n = 1 valve).
- rugulosa*, *Modiola* – Philippi, 1887a: 204 [1887b: 197], pl. 44, fig. 4. Lebu, Chile; Francisco J. Ovalle; Tertiary.
- rumphii*, *Modiola* – Philippi, 1847r: 114. East Indies. The Australian and Thailand *Modiolus rumphii* (Philippi, 1847) (Huber, 2010: 123, 553), or a synonym of *Modiolus rufus* (Fischer von Waldheim, 1807) (Huber, 2015: 366); Higo et al. (1999: 415) had listed it as a synonym of *Modiolus philippinarum* (Hanley, 1843).
- schythei*, *Modiola* – Philippi, 1887a: 203 [1887b: 196], pl. 44, fig. 6. Punta Arenas, Chile; Jorje Schythe; Tertiary. *Modiolus schythei* (Philippi, 1887) (Ihering, 1907: 346).
- siliqua*, *Modiola* – Philippi, 1849s: 28, *non* Matheron, 1843. Liewkiew Island [Ryukyu Islands, Japan]; Cécille via Largilliert. Syntype, MNHNS 50624 (n = 1) (33.7 mm x 15.6 mm). Possibly a synonym of *Modiolatus flavidus* (Dunker, 1857) (Huber, 2010: 556).
- solidus*, *Mytilus* – Philippi, 1899: 45–46, pl. 24, fig. 1. Doña Ana, Chile; [Mesozoic]. Syntype, SGO.PI.5016 (n = 1 valve).
- striatus*, *Mytilus* – Philippi, 1887a: 201 [1887b: 194], pl. 43, fig. 5, *non* Montagu, 1803, *non* Goldfuss, 1837. Lota (Volckmann) & south of Lebu, Chile; Tertiary. Syntype, SGO.PI.451 (n = 1 valve, erroneously labeled as “holotipo”, but this species was described from two localities).
- subcylindricus*, *Mytilus* “?” – Philippi, 1887a: 202 [1887b: 195], pl. 43, fig. 6. Punta Arenas, Chile; Jorje Schythe; Tertiary. Syntype, SGO.PI.447 (n = 1). *Mytilus subcylindricus* Philippi, 1887 (Ihering, 1907: 346).
- substriatus*, *Mytilus* – Philippi, 1847r: 119, *non* Münster, 1840. Locality unknown.
- teres*, *Modiola* – Philippi, 1846y: 148 [2], pl. 1, fig. 3. Indo-Pacific. The Indo-Pacific *Lithophaga teres* (Philippi, 1846) (Wilson, 1979: 439–447, pl. 16, figs. 1–3; Lamprell & Healey, 1998: 92–93, fig. 214; Higo et al., 1999: 420; Okutani, 2000: 876–877, fig. 74; Swennen et al., 2001: 64, fig. 18; Qi., 2004: 232, pl. 123J; Huber, 2010: 119; Kleemann & Maestrati, 2012: 75–78). Kleemann & Maestrati (2012) regarded this species as also occurring in the western Atlantic. Type material probably lost (Kleemann & Maestrati, 2012).
- vestita*, *Modiola* – Philippi, 1844g: 51, 300, pl. 15, fig. 12a–c. Malta. Synonym of *Lioberus agglutinans* (Cantraine, 1835) (Sabelli et al., 1990: 285; Huber, 2010: 556).
- vidali*, *Mytilus* – Philippi, 1887a: 203 [1887b: 196], pl. 44, fig. 13. Laguna de Vichuquen, Chile; Quaternary. Possible syntype, MNHNS 203. *Modiola vidali* (Philippi, 1887) (Letelier et al., 2003: 118).
- volckmanni*, *Mytilus* – Philippi, 1887a: 201 [1887b: 194], pl. 44, fig. 10. Puchoco (Volckmann) & Navidad, Chile; Tertiary. Syntypes, SGO.PI.444 (n = 1 valve, from Puchoco, labeled as “holotipo”); SGO.PI.440 (n = 1 valve, from Navidad).

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“*angustatus*, *Mytilus*” – Mörch (1874: 174–175) attributed this species name to “Philippi” based upon Philippi’s label with a specimen from the Magellan Strait (sent by Philippi to Möller in 1845), in the Zoological Museum (Kopenhagen). However, this name remained a manuscript name as Mörch did not provide a description. Philippi (1836a: 72) also described a “*M. galloprovincialis* var.  $\beta$  *angustatus*” from Sicily (see above).



- "*chiloensis*, *Mytilus*" – Reeve, 1857a: pl. 6, fig. 21, ex Philippi ms. This species was listed by Ruhoff (1980: 195) as being by "Philippi, in Reeve," but it was only a ms name in the Cuming collection.
- "*compressus*, *Mytilus*" – Reeve, 1857a: pl. 2, fig. 5, ex Philippi ms. This species was listed by Clessin (1887: 84–85, pl. 13, fig. 10) as a Philippi species, and by Ruhoff (1980: 205) as being by "Philippi, in Reeve," but it was only a ms name in the Cuming collection. Reeve's possible syntypes, NHMUK 1975107 ( $n = 2$ ); Philippi's own specimens are in ZMB 16566 ( $n = 3$  valves, Chiloe, Chile).
- "*opifex*, *Gregariella*" – Valdovinos (1999: 153) and Letelier et al. (2003: 118) attributed this species to "Philippi, 1847", but it was first described by Say, 1825.
- "*pusio*, *Mytilus* (*Chloromya*)" – Mörch (1874: 174–175), the first to describe this species, attributed this species name to "Philippi" based upon Philippi's label with a specimen from the Magellan Strait (sent by Philippi to Möller in 1845), in the Zoological Museum (Kobenhavn), but Mörch also recorded this species from Norway. Jeffreys (1879: 567), as first reviser, limited this species to the eastern Atlantic (Norway) (Lamy, 1936: 147, 154).
- "*triangulum*, *Modiola*" – Lamy (1936: 284) attributed this name as a "Koch mss." name in Philippi (1847r: 115), but it should be cited as "Koch, in Philippi."

## Arcidae

- acutangula*, *Arca* – Philippi, 1887a: 186 [1887b: 179–180], pl. 25, fig. 5. Hualpen, Chile; Cretaceous. Holotype, SGO.PI.653 ( $n = 1$  valve).
- amarali*, *Arca* – Philippi, 1899: 54, pl. 27, fig. 4. Cordillera de Tinguiririca; Moses Amaral; [Mesozoic].
- amygdalum*, *Arca* – Philippi, 1845p: 29–30 [5–6], pl. 2, fig. 2, *non* Link, 1807. "China". Albano et al. (2009) determined that this species, which recently invaded the Mediterranean Sea, was not from "China", and is instead a junior synonym of the western Atlantic *Anadara transversa* (Say, 1822) (see also Huber, 2010: 570). Unnecessarily renamed *Scapharca demiri* Piani, 1981, and formerly listed by Higo et al. (1999: 425) as a synonym of the Asian *Scapharca kagoshimensis* (Tokunaga, 1906).
- andina*, *Arca* – Philippi, 1899: 55, pl. 27, fig. 7. Portezuelo de Tinguiririca, Chile; Frid. Albert; [Mesozoic].
- arabica*, *Arca* – Philippi, 1847x: 28 [14], pl. 4, fig. 2. Red Sea. Figured syntype, MNHNS 50215 ( $n = 1$ ) (41.8 mm x 26.3 mm). Synonym of the Indo-Pacific *Arca avellana* Lamarck, 1819 (Oliver, 1992: 33, pl. 1, fig. 1a–c; Higo et al., 1999: 421), which in turn has recently been treated as a synonym of *Arca patriarchalis* Röding, 1798 (Huber, 2010: 129, 560).
- arteagae*, *Arca* – Philippi, 1897: 368–369, pl. 6. Between Punta Roble & Punta Pabellón, Isla Chiloé, Chile; [Cenozoic?].
- aspera*, *Arca* – Philippi, 1844g: 43, 299, pl. 15, fig. 1a–c. Lamati, Calabria, Italy; fossil. Synonym of *Asperarca nodulosa* (O. F. Müller, 1776) (Janssen, 1972: 13; La Perna, 1998: 11; Janssen & Krylova, 2014: 55).
- brandtii*, *Arca* – Philippi, 1845p: 29 [5], pl. 2, fig. 1. Locality unknown; Brandt. Synonym of the Panamic *Anadara multicostata* (G. B. Sowerby I, 1833) (Bernard, 1983: 15; Coan & Valentich-Scott, 2012: 179–180, pl. 58).
- bronnii*, *Arca* – Philippi, 1851b: 49–50. Java. Syntypes, MNHNS ( $n = 2$  specimens and 1 valve; no catalog number) (largest, 43.8 mm x 19.4 mm). Possibly a synonym of the Indo-Pacific *Tegillarca rhombea* (Born, 1778) (Huber, 2010: 141, 573).
- candidula*, *Arca* – Philippi, 1851b: 50. Locality unknown. Syntype, MNHNS 50272 ( $n = 1$  valve) (48.3 mm x 37.1 mm).
- caracolensis*, *Arca* – Philippi, 1899: 57, pl. 28, fig. 4. Caracoles, Chile; [Mesozoic].
- cecillii*, *Arca* – Philippi, 1849h: 131; 1849z: 85–86 [17–18], pl. 5, figs. 2, 3, as *A. "cecillei."* China; Largilliert. Synonym of the southwestern Pacific *Scapharca cornea* (Reeve, 1844); concerning the latter: Qi (2004, pl. 115D).
- cerastes*, *Arca* – Philippi, 1899: 58, pl. 28, fig. 10. Río Tinguiririca, Chile; [Mesozoic].
- chemnitzii*, *Arca* – Philippi, 1851b: 50–51. West Indies. The western Atlantic *Anadara chemnitzii* (Philippi, 1851) (Rios, 1994: 231, pl. 80, fig. 1142; Huber, 2010: 139; Tunnell et al., 2010: 309).
- chilensis*, *Arca* – Philippi, 1857: 406; 1887a: 187 [1887b: 181], pl. 36, fig. 6. Hacienda de La Cueva, Chile; Ignacio Domeyko; Tertiary [Pliocene]. Syntypes, SGO.PI.264 ( $n = 1$ , labeled as "lectotipo"), SGO.PI.4799–4802 ( $n = 3$ , labeled as "paralectotipo"); SGO.PI.268 is labeled as a "paralectotipo", but it was not collected until 1878, after the 1857 description. *Anadara* (*Rasia*) *chilensis* (Philippi, 1857) (Herm, 1969: 99, pl. 1, figs. 3, 4, as "1887"; DeVries & Frassinetti, 2003: 126, pl. 2, fig. 4; Nielsen, 2013: 50, figs. 8a–f).



- colchaguensis*, Arca “?” – Philippi, 1899: 56, pl. 28, fig. 2. “Cerro de Herrera” Colchagua, Chile; Guill. Krug; [Mesozoic].
- consanguinea*, Arca – Philippi, 1899: 55, pl. 27, fig. 8. Portezuelo de Tinguiririca, Chile; Frid. Albert; [Mesozoic].
- cornuta*, Arca – Philippi, 1899: 56, pl. 28, fig. 1. Doña Ana, Coquimbo, Chile; [Mesozoic].
- crassicornis*, Arca – Philippi, 1899: 58–59, pl. 28, fig. 11. Río Tinguiririca, Chile; [Mesozoic].
- cruciata*, Arca – Philippi, 1849z: 87–88 [19–20], pl. 5, fig. 7. Indian Ocean; Gruner. *Barbatia* (*Ustularca*) *cruciata* (Philippi, 1849) (Higo et al., 1999: 422; Okutani, 2000: 846–847, fig. 9); synonym of *Barbatia fusca* (Bruguière, 1789) [originally Arca, and junior homonym of *Arca fusca* Lightfoot, 1786, which is however a *nomen dubium*] (Agüera García & Oliver, 2008: 15–18, figs. 5e, 6i, 6j, 9a, 9b).
- curaumae*, Arca – Philippi, 1887a: 188 [1887b: 181], pl. 25, fig. 7. Hacienda Curauma near Valparaíso, Chile; Tertiary. Holotype, SGO. Pl.652 (n = 1 valve).
- dunkeri*, Arca – Philippi, 1845z: 448 [*nomen nudum*].
- elegans*, Arca – Philippi, 1847r: 92–93; 1849z: 86–87 [18–19], pl. 5, fig. 5. Yucatan, Mexico; Largilliert. Syntype, MNHNS 50230 (n = 1) (32.9 mm x 25.6 mm). Synonym of the western Atlantic *Eontia ponderosa* (Say, 1822).
- erythraeonensis*, Arca – Philippi, 1851b: 51, ex Jonas ms. Red Sea [as “Mare Erythraeum”]; Rodatz, via A. B. Meyer. Philippi specifically indicated that the name was taken from a Jonas manuscript. *Anadara erythraeonsis* (Philippi, 1851) (Oliver, 1992: 38, pl. 3, fig. 4a, b).
- glabrata*, Arca – Philippi, 1899: 52, pl. 26, fig. 3. Portezuelo de Tinguiririca, Chile; Frid. Albert; [Mesozoic].
- grandis*, Arca – Philippi, 1899: 52, pl. 26, figs. 1, 2, non Broderip & G. B. Sowerby I, 1829. Hacienda Valdivia, Chile; 4,000 m; Ovalle; Perry; Tertiary?
- granulata*, Arca – Philippi, 1847r: 92; 1850i: 114 [22], pl. 6, fig. 3. Hawaii; Griffith. Syntypes, MNHNS 240 (n = 2, larger, figured specimen is 41.0 mm x 23.5 mm). Synonym of *Barbatia lima* (Reeve, 1844) (Kay, 1979: 501–502, fig. 162A, B).
- hemidesmos*, Arca – Philippi, 1845p: 31–32 [7–8], pl. 2, fig. 5. Locality unknown. The western Atlantic *Anadara hemidesmos* (Philippi, 1845); type locality clarified as being Martinique (Huber, 2010: 136, 568).
- hispida*, Arca – Philippi, 1849z: 86 [18], pl. 5, fig. 4. Mergui Archipelago, Burma [Myanmar]; Th. Philippi. Syntype, MNHNS 50231 (n = 1) (31.8 mm x 27.5 mm). Synonym of *Scapharca inaequalis* (Bruguière, 1789) (Higo et al., 1999: 425), or more likely part of the species complex “*A. hispida*/*A. penangana* (Jousseaume, 1893)/*A. cistula* (Reeve, 1844)”, which is close to *Anadara inaequalis* but not synonym of the latter (Lutaenko & Volvenko, 2013: 89–91; Lutaenko, pers. commun., July 2013).
- involuta*, Arca “?” – Philippi, 1887a: 189 [1887b: 182], pl. 36, fig. 5. Chile; Francisco J. Ovalle collection; Tertiary.
- kraussii*, Arca – Philippi in Krauss, 1848: 14–15, pl. 1, fig. 13; Philippi, 1849z: 88 [20], pl. 5, figs. 8–10. On the one hand, Philippi provided Krauss with the species name and some comparative notes (D. G. Herbert, in litt., 15 Dec. 2015). On the other hand, the description is similar to other new species in Krauss’ volume, is not signed by Philippi, and refers to Philippi in the third person. Perhaps Krauss thought that the name had already been published in the *Abbildungen*, but it did not appear there until the following year. Possible syntypes, SMF 315103 (n = 2); syntype ZMB 111743 (n = 1, Natal, ex Krauss). Synonym of *Arca avellana* Lamarck, 1819 (Lutaenko, 2015: 128, pl. 1, figs. E–H).
- laevigata*, Arca – Philippi, 1899: 55–56, pl. 27, fig. 9. No locality provided, Chile; [Mesozoic].
- lamarckii*, Arca – Philippi, 1845i: 55. China. Syntype, MNHNS (n = 1, no catalog number) (57.1 mm x 38.4 mm). *Nomen dubium* (Huber, 2010: 566).
- lepida*, Arca – Philippi, 1899: 53, pl. 26, fig. 13. Tinguiririca, Chile; Frid. Albert; [Mesozoic].
- lirata*, Arca – Philippi, 1887a: 188 [1887b: 181], pl. 36, fig. 7 [plate caption as “*A. exilis*”]. Matanzas; Tertiary. Holotype, SGO. Pl.651 (n = 1 valve). *Anadara* (*Rasia*) *lirata* (Philippi, 1887); Miocene (del Río, 1991: 31–32, pl. 1, fig. 3, as 1893); late Miocene (Frassinetti & Covacevich, 1994: 77–78, figs. 3–5, as 1887; Martínez & del Río, 2002: 183).
- lirata*, Arca – Philippi, 1893b: 11, pl. 1, fig. 14, non Philippi, 1887a. Argentina; Tertiary. Synonym of *Anadara bonplandiana* (d’Orbigny, 1843) of the Tertiary of Argentina and Chile (Griffin & Nielsen, 2008: 260–261, pl. 2, figs. 10–11).
- listeri*, Arca – Philippi, 1849z: 87 [19], pl. 5, fig. 1. Jamaica. Synonym of *Barbatia cancellaria* (Lamarck, 1819) (Lamy, 1907: 56).



- mathiae*, *Arca* – Philippi, 1887a: 188 [1887b: 181], pl. 37, fig. 7. Lebu & Tucapel, Chile; Tertiary. Syntypes, SGO.PI.265 (n = 1, Lebu, labeled as "lectotipo"); SGO.PI.5053 (n = 1 valve, Lebu, labeled as "paralectotipo").
- musculosa*, *Arca* "?" – Philippi, 1887a: 187 [1887b: 180], pl. 38, fig. 7. Locality unknown, Chile; Museum collection. Possible syntype, SGO.PI.266 (n = 1, labeled as "holotipo" from "Coquimbo?").
- obliqua*, *Arca* – Philippi, 1844g: 43–44, 299, pl. 15, fig. 2, 2c, *non* Portlock, 1843, *non* Reeve, 1844. Lamati, Calabria, Italy; fossil. *Arca philippiana* Nyst, 1848, *nom. nov.* Also unnecessarily renamed as *Arca obliquata* Locard, 1899, *non* W. Wood, 1828, and this, in turn, as *Arca obliquatula* Dautzenberg, 1927. *Bathyarca philippiana* (Nyst, 1848) (Sabelli et al., 1990: 278). See ICZN Opinion 1887; 1998, with respect to the suppressed *Arca grenophila* Risso, 1826, although *Arca rari-dentata* S. V. Wood, 1840, may be an older name for this taxon (as listed in the synonymy by Kantor & Sysoev, 2005: 321).
- oblonga*, *Arca* – Philippi, 1849z: 85–86 [17–18], pl. 5, fig. 6, *non* Goldfuss, 1837. Mergui Archipelago, Burma [Myanmar]; Th. Philippi. Synonym of *Tegillarca granosa* (Linnaeus, 1758) (Higo et al., 1999: 426).
- occidentalis*, *Arca* – Philippi, 1847x: 29 [15], pl. 4, fig. 4. Cuba; Pfeiffer. Syntype, MNHNS (n = 1, no catalog number) (30.2 mm x 16.2 mm). Synonym of *Arca zebra* (Swainson, 1833) (Abbott, 1958: 109; Rios, 1994: 230, pl. 80, fig. 1135).
- oxytropis*, *Arca* – Philippi, 1887a: 188 [1887b: 182], pl. 37, fig. 6. Lebu, Chile; Tertiary. Syntypes, SGO.PI.650 (n = 1 valve, labeled as "lectotipo"); SGO.PI.5034 (n = 1 valve, labeled as "paralectotipo").
- pencana*, *Arca* – Philippi, 1887a: 186–187 [1887b: 180], pl. 58, fig. 10. Isla Quiriquina, Chile; Cretaceous. Holotype, SGO.PI.472 (n = 1 valve).
- perryi*, *Arca* – Philippi, 1899: 53, pl. 27, figs. 1, 2. Hacienda Valdivia, Chile; 4,000 m; Ovalle, Perry; [Mesozoic].
- plagemanni*, *Arca* – Philippi, 1899: 57–58, pl. 28, fig. 6. Cajon del Río Negro "?", Chile; [Mesozoic].
- platensis*, *Arca* – Philippi, 1893b: 11, pl. 1, fig. 8. Argentina; Tertiary. *Arca* (A.) *platensis* Philippi, 1893, Miocene (Ihering, 1907: 372; del Río, 1991: 30, pl. 1, fig. 2; del Río & Martínez, 1998: 49, pl. 16, figs. 1–2).
- pubigera*, *Arca* – Philippi, 1851b: 52. China; Cécille via Largilliert. Synonym of *Diluvarca ferruginea* (Reeve, 1844) (Higo et al., 1999: 426).
- reeveana*, *Arca* – Philippi, 1851b: 53, *non* d'Orbigny, 1846, *non* Nyst, 1848. Locality unknown.
- scolia*, *Arca* – Philippi, 1887a: 189 [1887b: 182], pl. 58, fig. 15. Lota, Chile; Volckmann; Tertiary.
- semilaevis*, *Arca* – Philippi, 1899: 52–53, pl. 26, fig. 4. Portezuelo de Tinguiririca, Chile; Frid. Albert; [Mesozoic].
- sinensis*, *Arca* – Philippi, 1851b: 53–54. China.
- speciosa*, *Arca* – Philippi, 1849h: 131–132; 1850i: 113 [21], pl. 6, fig. 1. Locality unknown. The poorly known *Anadara* (*Divuvarca*) *speciosa* (Philippi, 1849), which is possibly a junior synonym of western Pacific *A. (D.) tricenica* (Nyst, 1848) (Huber, 2010: 573).
- stelzneri*, *Arca* – Philippi, 1899: 54–55, pl. 27, fig. 6. Cordillera de Tinguiririca, Chile; Frid. Albert; [Mesozoic].
- stolpi*, *Arca* – Philippi, 1899: 55–56, pl. 28, fig. 3. Locality not specified, Chile; [Mesozoic].
- sublaevis*, *Arca* – Philippi, 1899: 54, pl. 27, fig. 5. Cordillera de Tinguiririca, Chile; Frid. Albert; [Mesozoic].
- subquadrangula*, *Arca* – Philippi, 1847k: 201 [10], pl. 3, fig. 3, ex Dunker ms. The description of this species was signed by Philippi, so it is interpreted to be a Dunker ms species. Amboina. Synonym of *Arca navicularis* Bruguière, 1797 (Higo et al., 1999: 421).
- valdiviana*, *Arca* – Philippi, 1887a: 187 [1887b: 180], pl. 40, fig. 1. Llancahue, Chile; W. Frick & Millanejo; Bolchmann; Tertiary. Syntypes, SGO.PI.494 (n = 1, from Llancahue, labeled as "lectotipo"); SGO.PI.4797, 4798 (n = 2, from Llancahue, labeled as "paralectotipo"); SGO.PI.428 (n = 1, from Millanejo). Synonym of *Anadara tuberculosa* (G. B. Sowerby I, 1833) (Bernard, 1983: 15).
- villaroeli*, *Arca* – Philippi, 1899: 57, pl. 28, fig. 5. Caracoles, Chile; [Mesozoic].
- volckmanni*, *Arca* – Philippi, 1887a: 189 [1887b: 182], pl. 25, fig. 6. Chiloé, Chile; Volckmann; Tertiary. Syntype, SGO.PI.649 (n = 1 valve).
- volckmanni*, *Arca* – Philippi, 1899: 58, pl. 28, fig. 7, *non* Philippi, 1887. Manflas "?", Chile; Volckmann.

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"*bicors*, *Arca*" – Ihering (1907: 449) credited this species to "(Jonas) R. A. Philippi, Abbild. Conch. II, 1847, Taf. 2, fig. 6," but it should instead be credited to Jonas in Philippi.



"*hemicardium*, *Arca*" – Bernard (1983: 16) credited this species to "Philippi, 1843: 43, pl. 1, fig. 1 (Koch MS.)," but it should instead be credited to Koch in Philippi, 1843c.

#### Cucullaeidae

*chilensis*, *Cucullaea* – Philippi, 1887a: 189–190 [1887b: 183], pl. 40, fig. 2. Isla Guaiteca ["perhaps" Huafo]; Juan Oyarzun, Matanzas, Lebu & Millanejo; Volckmann – all Chile; Tertiary. Syntypes, SGO.PI.349 (n = 1, figured specimen from Isla Guaiteca, labeled as "holotipo" and cited as "holotipo" by Frassinetti, 2001: 75); SGO.PI.348 (n = 1 valve, Matanzas); SGO.PI.350 (n = 1, Millanejo); SGO.PI.426 (n = 1 valve, Lebu). *Cucullaea chilensis* Philippi, 1887; Miocene (Frassinetti & Covacevich, 1994: 78–79, fig. 6).

*darwini*, *Arca* – Philippi, 1887a: 188 [1887b: 181], pl. 36, fig. 3. Santa Cruz; Ramón Vidal Gormáz; Tertiary. Holotype, SGO.PI.269 (n = 1 valve). *Cucullaea darwini* (Philippi, 1887), Miocene (Tavera, 1979: 84–85); Oligocene–Miocene (Frassinetti & Covacevich, 1999: 18, pl. 2, fig. 16).

*fricki*, *Cucullaea* – Philippi, 1887a: 190 [1887b: 183], pl. 37, fig. 2. Llancahue, Chile; W. Frick; Tertiary.

#### Glycymerididae

*araucanus*, *Pectunculus* – Philippi, 1887a: 191 [1887b: 184], pl. 36, fig. 2. Lebu, Chile; Volckmann; Tertiary. *Glycymeris araucanus* (Philippi, 1887); type material not found (Frassinetti & Covacevich, 1984: 111, fig. 30).

*concinus*, *Pectunculus* – Philippi, 1845i: 55–56. Pacific Ocean. Synonym of the eastern Pacific *G. gigantea* (Reeve, 1843) (Huber, 2010: Chapter 5 on CD).

*crassus*, *Pectunculus* – Philippi, 1841f: 13; 1844z4: 13, 47, 71. Tertiary near Wilhelms-höhe, Hessen, Germany [Late Oligocene]. Synonym of *Glycymeris obovata* (Lamarck, 1819) (Janssen, 1979b: 32–35, pl. 1, figs. 17, 18). Type material lost (R. Janssen, pers. comm., April 2013).

*hirtus*, *Pectunculus* – Philippi, 1846z2: 191. Cumana, Venezuela. Synonym of the western Atlantic *Glycymeris marmorata* (Gmelin, 1791) (Huber, 2010: 151, 583).

*ibari*, *Pectunculus* – Philippi, 1887a: 190 [1887b: 183–184], pl. 40, fig. 3. Punta Arenas, Chile; Tertiary. Holotype, SGO.PI.261. *Glycymeris (Glycymerita) ibari* (Philippi,

1887) (Frassinetti & Covacevich, 1984: 119–120, figs. 24–28, 31, 32, 35, 36; Griffin, 1991: 126).

*lineatus*, *Pectunculus* – Philippi, 1836a: viii, 62, pl. 5, fig. 4; 1844g: 44. Messina, Sicily, Italy; Petrus Campanella. Synonym of *Glycymeris glycymeris* (Linnaeus, 1758) (Sabelli et al., 1990: 279), or of *Glycymeris bimaculata* (Poli, 1795) (Huber, 2010: 150, 581).

*magellanicus*, *Pectunculus* – Philippi, 1887a: 190–191 [1887b: 184], pl. 41, fig. 1. Punta Arenas, Chile; Tertiary. Lectotype, SGO.PI.258, designated by Frassinetti & Covacevich (1984: 119–120, figs. 31–32); paralectotypes SGO 4147 (n = 1 valve); SGO 258 (n = 1 valve). Synonym of *Glycymeris (Glycymerita) ibari* (Philippi, 1887) (Fuenzalida, 1942: 407; Frassinetti & Covacevich, 1984: 119–120, figs. 24–28, 31, 32, 35, 36).

*scutulatus*, *Pectunculus* – Philippi, 1851c: 90–91. Formosa; Largilliert. Type material not found in Muséum de Rouen (Muséum de Rouen 143204031 has four specimens, but this species was described from a single specimen). Synonym of the western Pacific *Glycymeris flammea* (Reeve, 1843) (Huber, 2010: 150, 583).

*symmetrica*, *Lucina* – Philippi, 1893b: 9, pl. 1, fig. 3. Argentina; Tertiary. "Holotipo MACN 2637" (del Río, 1991: 42, fig. 12). *Glycymeris (G.) symmetricus* (Philippi, 1893); Miocene (Ihering, 1907: 372; del Río, 1991: 42, fig. 12; del Río & Martínez, 1998: 52, pl. 16, fig. 20).

#### Limopsidae

*araucanus*, *Limopsis* – Philippi, 1887a: 191 [1887b: 184], pl. 46, fig. 4. Llancahue, Chile; Wilhelm Frick; Tertiary. Syntypes, SGO.PI.629 (n = 1 valve, labeled as "lectotipo"); SGO.PI.4847 (n = 1 valve, labeled as "paralectotipo"). *Limopsis araucanus* Philippi, 1887; Miocene (Tavera, 1979: 85–86).

*minutus*, *Pectunculus* – Philippi, 1836a: viii, 63, pl. 5, fig. 3a, 3b; 1844g: 45. Palermo, Sicily, Italy; fossil. The eastern Atlantic *Limopsis minuta* (Philippi, 1836) (Sabelli et al., 1990: 279; Kantor & Sysoev, 2005: 315; Huber, 2010: 589; Janssen & Krylova, 2014: 56), which has also been reported from the western Atlantic (Rios, 1994: 233, pl. 81, fig. 1152; Mikkelsen & Bieler, 2007: 70; Tunnell et al., 2010: 311); *Limopsis (Paracritis) minuta* (Philippi, 1836) (Huber, 2010: 586; Janssen, 2015: 25). Syntypes, PHB MB M.6318 (51) 13



( $n = 3$ , from Asti); PHB MB M.552 (51) 13 ( $n = 1$  valve). Philippi's use of this species name for Eocene fossils from Germany (Philippi, 1841f: 14; 1844z4: 14, 48, 72) was in error, as those records are instead referable to *Cosmetopsis retifera retifera* (Semper 1861) (Janssen, 2015: 14–15).

*pygmaeus*, *Pectunculus* – Philippi, 1836a: viii, 63, pl. 5, fig. 5a, 5b, *non* Lamarck, 1819; 1844g: 45; Philippi, 1845z: 448. Militello, Sicily, Italy; fossil. Possible syntypes, PHB MB M.548 (V) 9 ( $n = 1$ ); PHB MB M.549 (V) 9 ( $n = 1$ ) (missing in 2013). *Limopsis friedbergi* Glibert & van de Poel, 1965a: 74–75, *nom. nov.*, as *Limopsis (Limarca) anomala friedbergi*. Listed by Sabelli et al. (1990: 279) as *Limopsis pygmaea* (Philippi, 1836), but noting the homonymy.

#### Philobryidae

*miliaris*, *Pectunculus* – Philippi, 1845i: 56. Strait of Magellan, Chile. *Lissarca miliaris* (Philippi, 1845) (Carcelles & Williamson, 1951: 327; Bernard, 1983: 17; Dell, 1990: 33, 28, fig. 45; Valdovinos, 1999: 152; Narchi et al., 2002: 657–658, figs. 17–19; Zelaya, 2016: 254).

#### Inoceramidae

*diazi*, *Inoceramus* – Philippi, 1899: 44, pl. 23, fig. 3. Caracoles, Chile; Wenceslao Díaz; [Mesozoic].

*dispar*, *Inoceramus* “?” or *Aucella* “?” – Philippi, 1899: 96–97, pl. 42, fig. 1a, b. Locality unknown, Chile; [Mesozoic]. Syntype, SGO.PI.925 ( $n = 1$  valve, label gives locality as “Tarapacá?”).

*glaber*, *Inoceramus* – Philippi, 1899: 44, pl. 23, fig. 4. Locality unknown, Chile; Carlos Stolp; [Mesozoic].

*patagonicus*, *Inoceramus* – Philippi, 1899: 43–44, pl. 23, fig. 2. Cordillera del Viento, east of Nevada de Chillan, Chile; Manuel Arístides Zañartu; [Mesozoic]. Neotype, MLP 23388 (W4), late Bathonian (Steinmanni Zone) beds at Chacay Melehue, Cordillera del Viento, Neuquen, Argentina; designated by Damborenea (1990: 744, figs. 10.4–10.6, 11.3). *Retroceramus patagonicus* (Philippi, 1899).

*vallenarensis*, *Inoceramus* “?” – Philippi, 1899: 43, pl. 23, fig. 1. Andibus de Vallenar, [Coquimbo], Chile; J. M. Reyes; [Mesozoic]. Syntype, SGO.PI.924 ( $n = 1$  valve).

#### Pteriidae

*alberti*, *Avicula* – Philippi, 1899: 40, pl. 21, fig. 3. Valle del Tinguiririca, [Colchagua], Chile; Frid. Albert; [Mesozoic]. Syntype, SGO.PI.923 ( $n = 1$  valve).

*aluco*, *Avicula* – Philippi, 1849r: 20. Cuba. Syntype, MNHNS 51108 ( $n = 1$  valve) (40.6 mm x 28.1 mm).

*andina*, *Avicula* “?” – Philippi, 1899: 40, pl. 21, fig. 5. Valle del Tinguiririca “?”, [Colchagua], Chile; C. Stolp; [Mesozoic]. Syntype, SGO.PI.921 ( $n = 1$  valve) (this lot is a block that also has the syntype of *Gervillia chilensis* Philippi, 1899 [Bakevillidae]).

*canarina*, *Avicula radiata* – Philippi, 1849r: 22. Yucatan; Largilliert.

*chemnitzii*, *Avicula* – Philippi, 1849r: 19–20. China; E. B. Philippi. The Indo-Pacific *Pinctada chemnitzii* (Philippi, 1849) (Ranson, 1961: 40–44, pls. 23, 24, text-figs. 11, 12, as *P. “chemnitzii”*; Lamprell & Healey, 1998: 104–105, fig. 251; Higo et al., 1999: 431; Okutani, 2000: 882–883, fig. 14; Huber, 2010: 169).

*chloris*, *Avicula* – Philippi, 1851b: 54. Yucatan; Largilliert. Type material not found in Muséum de Rouen; *nomen dubium* (Huber, 2015: Chapter 5 on CD).

*colchaguensis*, *Avicula* “?” – Philippi, 1899: 40, pl. 21, fig. 2. Valle del Tinguiririca, [Colchagua], Chile; C. Stolp; [Mesozoic]. Syntype, SGO.PI.922 ( $n = 1$  valve).

*elegans*, *Crenatula* – Philippi, 1851b: 68. Red Sea; A. B. Meyer. Synonym of the Indo-Pacific *Crenatula picta* (Gmelin, 1791).

*euryptera*, *Avicula* – Philippi, 1899: 39–40, pl. 21, fig. 1. Portezuelo del Tinguiririca, Chile; [Mesozoic].

*inflata*, *Crenatula* – Philippi, 1851b: 68–69. Locality unknown. Synonym of the Indo-Pacific *Crenatula picta* (Gmelin, 1791).

*largillierti*, *Avicula* – Philippi, 1849h: 133. Basilan, Philippine Islands; Largilliert. Syntype, MNHNS 51091 ( $n = 1$ , from Basilan) (93.9 mm x 44.0 mm). Possible senior synonym of *Pteria peasei* (Dunker, 1872); treated as a *nomen dubium* by Huber (2010: 168, 601).

*laticauda*, *Avicula* – Philippi, 1849r: 20. China; E. B. Philippi. Syntypes, MNHNS 51116 ( $n = 2$  valves) (larger valve 67.8 mm x 62.9 mm).

*marmorata*, *Avicula* – Philippi, 1849r: 20–21. China; E. B. Philippi. Possible syntype, MNHNS 51089 ( $n = 1$ ), but written on inside of shell is “*Avicula semisagitta* – Africa” so the specimen and the label do not match.



*pica*, *Avicula* – Philippi, 1849r: 21. China; Largilliert. Syntypes, MNHNS 51093 (2 specimens + 1 valve) (largest, 33.7 mm x 34.9 mm).

*psittacus*, *Avicula* – Philippi, 1849r: 21. Antilles; Gruner & Jamaica; E. B. Philippi.

*strix*, *Avicula* – Philippi, 1849r: 22. Sargassi; E. B. Philippi. Syntype, MNHNS 51092 (n = 1 valve) (31.5 mm x 14.9 mm).

*turdus*, *Avicula* – Philippi, 1851b: 55. China.

#### Bakevellidae

*Plagia* – Philippi, 1899: 41–42, *non* Meigen, 1838 [Insecta: Diptera]. Type species (M): *Plagia andina* Philippi, 1899. Mesozoic; Chile. Possible synonym of *Bakevellia* King, 1848 (Cox, 1969a: N306).

*andina*, *Plagia* – Philippi, 1899: 42, pl. 22, fig. 4. Doña Ana, Coquimbo, Chile; Mesozoic.

*chilensis*, *Gervillia* – Philippi, 1899: 43, pl. 22, fig. 7. Valle de Tinguiririca “?”, Chile; Carlos Stolp; [Mesozoic]. Syntype, SGO.PI.921 (n = 1 valve) (this lot is a block that also has the syntype of *Avicula andina* Philippi, 1899 [Pteriidae]).

*copiapina*, *Gervillia* “?” – Philippi, 1899: 42, pl. 22, fig. 5. Juntas de Manflas, Chile; Volckmann; [Mesozoic]. Syntype, SGO.PI.931 (n = 1).

*mytiloides*, *Gervillia* “?” – Philippi, 1899: 42–43, pl. 22, fig. 6. Caracoles, Chile; Udalrico Prado; [Mesozoic].

#### Isognomonidae

*Hippochaeta* – Philippi, 1844g: 55, ex Sangiovanni ms, as “*Hippochaetae*”. Published in the synonymy of *Perna*. Type species (M): *Perna soldanii* Deshayes, 1836 (= *Perna maxillata* Lamarck, 1801, fide Zilch, 1938: 365). Under ICZN Code Article 11.6.1 (1999), available through its use as a valid name before 1961 by Zilch (1938: 365), as *Hypochaeta*, an incorrect subsequent spelling and a senior homonym of *Hypochaeta* Brauer & Bergenstamm, 1890 [Diptera]. Sangiovanni’s manuscript name was first rendered as “*d’ippocheta*” by Pilla (1833: 18), and subsequently rendered as *Hippochaeta* by Oken (1843: 47), but without any included species. Now treated as a subgenus of *Isognomon* Lightfoot, 1786 (e.g., Cox, 1969b: N322).

*araucana*, *Melina* – Philippi, 1887a: 208 [1887b: 201], pl. 45, fig. 4. Lebu; Tertiary. Ho-

lotype, SGO.PI.634 (n = 1 valve). Synonym of *Isognomon gaudichaudii* (d’Orbigny, 1843) (Bernard, 1983: 22).

*aviculiformis*, *Crenatula* – Philippi, 1887a: 207 [1887b: 200], pl. 45, fig. 7. Navidad & Lebu, Chile; Tertiary [Miocene]. *Neopan is aviculiformis* (Philippi, 1887); syntypes, SGO.PI.636, figured syntype (labeled as “lectotipo”) (Beu, 2004: 160); SGO.PI.635 (n = 2 valves, labeled as “paralectotipo”).

*chilensis*, *Avicula* – Philippi, 1887a: 206–207 [1887b: 199], pl. 45, fig. 1. Lebu, Chile; Tertiary [Miocene]. *Neopan is chilensis* (Philippi, 1887); SGO.PI.467, holotype (Beu, 2004: 160).

*pusilla*, *Melina* – Philippi, 1887a: 208 [1887b: 201], pl. 45, fig. 5, *non* Roemer, 1839. Matanzas, Chile; Tertiary. Holotype, SGO.PI.628 (n = 1). Possibly a junior synonym of *Isognomon gaudichaudi* (d’Orbigny, 1843) (Bernard, 1983: 22; Griffin & Nielsen, 2008: 268, figs. 6–8).

*stolpi*, *Perna* – Philippi, 1899: 45, pl. 23, fig. 5. Cordillera del Tinguiririca, Chile; C. Stolp; [Mesozoic]. Syntype, SGO.PI.929 (n = 1).

*subaurita*, *Perna* – Philippi, 1899: 44–45, pl. 21, fig. 4. Portezuelo del Tinguiririca, Chile; Frid. Albert; [Mesozoic].

#### Pinnidae

*andina*, *Pinna* – Philippi, 1899: 51, pl. 25, fig. 4. Cordillera de Tinguiririca, Chile; Nestor Calderon; [Mesozoic]. Syntype, SGO.PI.915 (n = 1 valve).

*angusta*, *Pinna* – Philippi, 1899: 51, pl. 25, figs. 2, 3. Portezuelo de Tinguiririca, Chile; [Mesozoic]. Syntypes, SGO.PI.913, 914 (n = 2).

*costata*, *Pinna* – Philippi, 1887a: 206 [1887b: 199], pl. 43, fig. 9, 9b, *non* Phillips, 1836. Llancahue, Chile; Wilhelm Frick; Tertiary. Holotype, SGO.PI.475 (n = 1).

*semicostata*, *Pinna* – Philippi, 1887a: 206 [1887b: 199], pl. 43, fig. 10, 10b, *non* Conrad, 1837. Navidad, Chile; Tertiary [Miocene]. Possible syntypes, SGO.PI.479 (n = 3, from Navidad); SGO.PI.478 is labeled as “holotipo”, but it is from Matanzas, which is not the type locality. *Pinna semicostata* Philippi, 1887; Miocene (Frassinetti, 2001: 76), but renaming required due to the homonymy.

*squamosissima*, *Pinna* – Philippi, 1849i: 164; 1849z5: 454. Carolina & Texas. Synonym of the western Atlantic *Atrina* (*Servatrina*) *serrata* (G. B. Sowerby I, 1825) (Schultz & Huber, 2013: 42–43, 160).



*truncata*, *Pinna* – Philippi, 1844g: 54, 300, pl. 16, fig. 1. Catania. Syntype, MNHNS 51176 (n = 1) (22 cm x 10 cm). Synonym of *Atrina fragilis* (Pennant, 1777) (Schultz & Huber, 2013: 27–29, 160).

*tumida*, *Pinna* – Philippi, 1887a: 206 [1887b: 198–199], pl. 43, fig. 8, 8b. Lebu, Chile; Tertiary. Holotype, SGO.PI.473 (n = 1).

*tumida*, *Pinna* – Philippi, 1899: 50–51, pl. 25, fig. 1, *non* Philippi, 1887. Tinguiririca, Chile; Bruno Amaral; [Mesozoic].

#### Ostreidae

*adglutinas*, *Ostrea* – Philippi, 1893b: 14, pl. 3, fig. 2, ex Bravard ms. Argentina; Tertiary. Synonym of *Ostrea patagonica* d'Orbigny, 1839; Miocene (del Río & Martínez, 1998: 54–55, pl. 7, figs. 5–6).

*adsociata*, *Ostrea* – Philippi, 1893b: 14, pl. 2, fig. 1. Argentina; Tertiary. Synonym of *Ostrea patagonica* d'Orbigny, 1839; Miocene (del Río & Martínez, 1998: 54–55, pl. 7, figs. 5–6), or of *Ostrea parasitica* Gmelin, 1791 (Ihering, 1907: 374–375).

*atacamensis*, *Ostrea* (*Exogyra*?) – Philippi, 1860a: 145 [1860b: 127–128], Petref. pl. 1, figs. 11, 12; 1899: 5, pl. 3, fig. 4. Desierto de Atacama, Chile; fossil. Cretaceous, possibly in *Amphidonte* (*Ceratostreon*) (Rubilar, 2008: 37).

*bravardi*, *Ostrea* – Philippi, 1893b: 13, pl. 4, fig. 2. Argentina; Tertiary. Synonym of *Ostrea patagonica* d'Orbigny, 1839; Miocene (Ihering, 1907: 373–374; del Río & Martínez, 1998: 54–55, pl. 7, figs. 5–6).

*burmeisteri*, *Ostrea* – Philippi, 1893b: 13, pl. 4, fig. 1. Argentina; Tertiary. Synonym of *Ostrea patagonica* d'Orbigny, 1839; Miocene (Ihering, 1907: 373–374; del Río & Martínez, 1998: 54–55, pl. 7, figs. 5–6).

*calocrepis*, *Ostrea* – Philippi, 1899: 7, pl. 1, fig. 4. Mountains, Chile; Frid. Albert; fossil. Cretaceous, possibly in *Amphidonte* (*Ceratostreon*) (Rubilar, 2008: 37).

*crassa*, *Ostrea* – Philippi, 1899: 8–9, pl. 8, fig. 2, *non* Defrance, 1821. Portezuelo del Tinguiririca, Chile; Fr. Albert; [Mesozoic].

*cymatodes*, *Ostrea* – Philippi, 1887a: 215 [1887b: 208], “pl. 45, fig. 9” [but not on pl.]. “Tumbez”; Cretaceous.

*depressa*, *Ostrea* – Philippi, 1836a: ix, 89, pl. 6, fig. 3; 1844g: 63. Sicily, Italy. Also fossil. Synonym of *Ostrea edulis* Linnaeus, 1758 (Sabelli et al., 1990: 298; Kantor & Sysoev, 2005: 322).

*longa*, *Ostrea* – Philippi, 1893b: 14, pl. 3, fig. 1. Argentina; Tertiary. Synonym of *Ostrea patagonica* d'Orbigny, 1839; Miocene (del Río & Martínez, 1998: 54–55, pl. 7, figs. 5–6).

*palaris*, *Ostrea* – Philippi, 1899: 6, pl. 8, fig. 1. Río Tinguiririca, Chile; C. Stolp; [Mesozoic].

*praegrandis*, *Ostrea* – Philippi, 1844g: 64, 300, pl. 17 [entire pl.]. Nasiti, Calabria, Italy; fossil.

*pugae*, *Ostrea* – Philippi, 1899: 4–5, pl. 1, fig. 6a, 6b. Andes, Chile; Frid. Puga; [Mesozoic].

*pulla*, *Ostrea* – Philippi, 1899: 5, pl. 2, fig. 4. No locality given, Chile; [Mesozoic].

*remondi*, *Ostrea* – Philippi, 1887a: 214 [1887b: 207], pl. 48, fig. 4. Coquimbo, Chile; Rémond; Tertiary.

*rotunda*, *Ostrea* – Philippi, 1899: 4, pl. 1, fig. 5. Vallenar, Chile; J. M. Reyes; [Mesozoic].

*stolpi*, *Ostrea* – Philippi, 1899: 5–6, pl. 6, fig. 2. Cordillera de Santiago, Chile; Carlos Stolp; [Mesozoic].

*striata*, *Ostrea* (*Gryphaea*?) – Philippi, 1860a: 144–145 [1860b: 127], Petref. pl. 1, fig. 10; 1899: 6, pl. 6, fig. 3. Desierto de Atacama, Chile; [Mesozoic].

*tenuis*, *Ostrea* – Philippi, 1887a: 214–215 [1887b: 207], pl. 47, fig. 6a–c, 2 “?”, *non* Gmelin, 1791. Coquimbo & Lebu “?”, Chile; Tertiary. Syntypes, SGO.PI.380 (n = 1 valve, from Coquimbo, labeled as “lectotipo”); SGO.PI.4822–4827 (n = 5 valves, from Coquimbo, labeled as “paralectotipo”); SGO.PI.381 (n = 1 valve, from Lebu); SGO.PI.4828 (n = 1 valve, from Lebu). Synonym of *Ostrea* (*Ostrea*) *ferrarisii* d'Orbigny, 1839, Pliocene (Herm, 1969: 111–112, pl. 6, fig. 4, pl. 7, fig. 1).

*torresi*, *Ostrea* – Philippi, 1887a: 215 [1887b: 208], pl. 48, fig. 8 [as “fig. 9” in text.]. Strait of Magellan, Chile; Lorenzo Rodrigues & Diego Torres. Syntype, SGO.PI.429 (n = 1 valve). *Ostrea torresi* Philippi, 1887 (Ihering, 1905: 19–20; 1907: 345–346; Steinmann & Wilckens, 1908: 21–24, pl. 1, fig. 4, pl. 2, fig. 2).

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“*chilensis*, *Ostrea*” – Philippi, 1844. This species name first appeared in the general bivalve (and brachiopod) monograph by Küster (1843–1868), becoming available as a result of a caption on the issue cover to Lieferung 45 (one of the few covers known and its significance recognized) and plate 13 depicting the species which was issued in Lieferung 46, also in 1844). While this has been recognized as “Philippi in Küster” (Marshall, 2002), the



mere listing of this name by Küster means that under ICZN Code Article 50.1 (1999) the authorship should be credited to Küster, 1844. Although not required by the Code, it is best to render this as “Küster, 1844, ex Philippi ms.” to avoid any confusion. The text for this species (Küster, 1843–1868: 74–75) was not published until 1868 and clearly indicated this species as being a manuscript name (“Philippi in litt”). Toro (1995) provided a bibliography on the Chilean literature of this species, now classified in *Tiostrea* by some authors; Jeffs & Creese (1996) did the same for the New Zealand literature. Beu (2006: 210–211) reviewed the recent literature on the hypotheses for rafting of this species (which broods and does not have planktonic larvae) from Chile to New Zealand or vice versa, and concluded that: “It did not evolve here [New Zealand]; there are definitely no similar oysters in older New Zealand Miocene rocks. An origin in South America therefore seems more likely than one in New Zealand, but must be considered essentially uninvestigated ... Of course, an ultimate origin outside both New Zealand and Chile is equally likely, and would not rule out geologically recent rafting from New Zealand to Chile.” In the 1960s, this species was deliberately introduced into Wales (U.K.) for aquaculture purposes, and subsequently spread elsewhere in the U.K. (Morgan & Richardson, 2012).

#### Gryphaeidae

- carinata*, *Gryphaea* – Philippi, 1899: 12, pl. 5, fig. 2. Juntas de Manflas, Chile; [Mesozoic].  
*Gryphaea oxytropis* Philippi, 1899, Jurassic (Rubilar, 2005: 186, 192–194; 2008: 35).  
*cochlear*, *Exogyra* – Philippi, 1899: 17, pl. 7, fig. 6. Portezuelo de Tinguiririca, Chile; Frid. Albert; [Mesozoic]. Synonym of *Nanogyra nana* (J. Sowerby, 1822); Jurassic (Sha et al., 2002: 440–442).  
*curvirostris*, *Exogyra* – Philippi, 1899: 16, pl. 6, fig. 5. Valle del Tinguiririca, Chile; Carlos Stolp; [Mesozoic].  
*oxytropis*, *Gryphaea* – Philippi, 1899: 12, pl. 5, fig. 1. Chile; Volckmann; [Mesozoic]. Holotype, SGO.PI.5015 (n = 1 valve) (Rubilar, 2005: pl. 5, figs. 1a, 1b). *Gryphaea oxytropis* Philippi, 1899; Jurassic (Rubilar, 2005: 186, 192–194; 2008: 35).  
*palumbus*, *Exogyra* – Philippi, 1899: 16, pl. 6, fig. 1a, 1b. Doña Ana, Chile; Federico Philippi; [Mesozoic].

- punguis*, *Exogyra* – Philippi, 1899: 17, pl. 7, figs. 3, 5. Portezuelo de Tinguiririca, Chile; Frid. Albert; [Mesozoic]. Syntypes, SGO.PI.920 (n = 1 valve, specimen in fig. 3); SGO.PI.5017 (n = 1 valve, specimen in figure 5). Synonym of *Nanogyra nana* (J. Sowerby, 1822); Jurassic (Sha et al., 2002: 440–442).  
*regularis*, *Gryphaea* – Philippi, 1899: 14, pl. 21, fig. 6. Chile; [Mesozoic].  
*rostrata*, *Gryphaea* – Philippi, 1899: 11, pl. 3, fig. 3. Andes de Vallenar, Chile; José M. Reyes; [Jurassic]. Aberhan (1994: 34) noted that the “fragmented specimen defined as *G. rostrata* ... very likely comes from the same locality as the type material of *G. tricarinata*. It may be synonymous with the latter ... Due to the fragmentary nature and poor description of the type material of both species a clear statement is impossible at this point.”  
*scaphidium*, *Exogyra* – Philippi, 1899: 17, pl. 7, fig. 2. Portezuelo de Tinguiririca, Chile; Frid. Albert; [Mesozoic]. Figured syntype, SGO.PI.5018 (n = 1 valve).  
*schulzei*, *Gryphaea* – Philippi, 1899: 14, pl. 25, fig. 7. Copaquirí, Tarapacá, Chile; Johannes Schulze; [Mesozoic]. *Gryphaea oxytropis* Philippi, 1899, Jurassic (Rubilar, 2005: 186, 192–194; 2008: 35).  
*tricarinata*, *Gryphaea* – Philippi, 1899: 12–13, pl. 5, fig. 3. Andibus de Vallenar, Chile; J. M. Reyes; [Mesozoic]. *Gryphaea (Bilobissa) tricarinata* Philippi, 1899; Jurassic (Aberhan, 1994: 33–34, pl. 13, figs. 3–7), or *Gryphaea oxytropis* Philippi, 1899, Jurassic (Rubilar, 2005: 186, 192–194; 2008: 35).  
*trisulcata*, *Gryphaea* – Philippi, 1899: 14–15, pl. 42, fig. 2. Tarapacá, Chile; [Mesozoic].

#### Anomiidae

- Osteophorus* – Philippi, 1893b: 14–15, ex Bravard ms, non Meyer, 1857 [Amphibia]. Type species (M): *Osteophorus papyraceus* Philippi, 1893. Argentina; Tertiary. Junior synonym of *Pododesmus* Philippi, 1837 (del Río & Martínez, 1998: 60).  
*Pododesmus* – Philippi, 1837a: 385–387; 1837b: 9–10. Type species (M): *Pododesmus decipiens* Philippi, 1837, = *Placunanomia rudis* Broderip, 1834. Recent, western Atlantic.  
*antiqua*, *Anomia* – Philippi, 1899: 18, pl. 8, fig. 5. Arauco Province, Chile; [Mesozoic]. Syntype, SGO.PI.919 (n = 1 valve).  
*aspera*, *Anomia* – Philippi, 1844g: 65, 300, pl. 18, fig. 4. Sicily, Italy. Synonym of *Anomia ehippium* Linnaeus, 1758 (Sabelli et al.,



- 1990: 295; Huber, 2010: 616, in part as "aspera").
- asperella*, *Anomia* – Philippi, 1844z4: 50, 72, [86], pl. 2, fig. 12. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. Synonym of *Pododesmus* (*Heteranomia*) *squamula* (Linnaeus, 1758) (Janssen, 1979b: 68; Rust, 1999: 42).
- bullata*, *Ostrea* – Philippi, 1841f: 16–17; 1844z4: 16–17, [87], pl. 2, fig. 17. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. Synonym of *Anomia ephippium* Linnaeus, 1758 (Janssen, 1979b: 65–66, who dated Philippi's species from 1843). Type material lost (R. Janssen, pers. comm., April 2013).
- chinensis*, *Anomia* – Philippi, 1849h: 130–131; 1850n: 132 [1], pl. 1, fig. 1. China; Largilliert. Syntypes, MNHN Paris (3 valves, largest 40.4 mm x 34.4 mm, + 3 fragments); MNHNS 221 (n = 1 valve) (61.7 mm x 55.5 mm). The southeast Asian *Anomia chinensis* Philippi, 1849 (Bernard, 1983: 27, 68; Higo et al., 1999: 452; Okutani, 2000: 920–921, fig. 74; Swennen et al., 2001: 75, fig. 1; Qi, 2004: 250, pl. 138C; Huber, 2010: 188, 616).
- crepiduliformis*, *Anomia* – Philippi, 1887a: 216 [1887b: 209], pl. 47, fig. 8. Navidad, Chile; Tertiary [Miocene].
- decipiens*, *Pododesmus* – Philippi, 1837a: 386–387, pl. 9, figs. 1a–c; 1837b: 9–10. Havana, Cuba; [E.B. Philippi; "durch meinen jüngern Bruder"]. Synonym of the western Atlantic *Placunanomia rudis* Broderip, 1834 (Carcelles, 1941: 6).
- elegans*, *Anomia* – Philippi, 1844g: 65, 300, pl. 18, fig. 2. Sicily, Italy. Synonym of *Pododesmus patelliformis* (Linnaeus, 1761) (Sabelli et al., 1990: 296; Kantor & Sysoev, 2005: 326); some workers place this species in *Monia*.
- papyraceus*, *Osteophorus* – Philippi, 1893b: 14–15, pl. 4, fig. 3. Argentina; Tertiary. *Pododesmus papyraceus* (Philippi, 1893); late Miocene (Ihering, 1907: 379; del Río & Martínez, 1998: 60, pl. 17, figs. 4–6, pl. 25, figs. 2–3; Martínez & del Río, 2002: 178).
- polymorpha*, *Anomia* – Philippi, 1836a: ix, 92–93; 1844g: 65, 66. Sicily, Italy. Also fossil. Synonym of *Anomia ephippium* Linnaeus, 1758 (Sabelli et al., 1990: 295, as "pars"; Huber, 2010: 616). Possible syntypes, SMF 315508 (n = 1 specimen + 5 valves; Mediterranean, ex Philippi).
- scabrella*, *Anomia* – Philippi, 1836a: ix, 92; 1837c: 286, misspelled as "scabricula"; 1844g: 63, 300, pl. 18, fig. 1a, 1b. Sicily, Italy. Synonym

of *Anomia ephippium* Linnaeus, 1758 (Sabelli et al., 1990: 295). Syntypes, ZMB 15973 (6 valves) (largest 40.5 mm x 32.3 mm).

*venusta*, *Anomia* – Philippi, 1850n: 132 [2], pl. 1, fig. 5. Lapland & Norway, North Atlantic. Synonym of the northeastern Atlantic *Heteranomia squamula* (Linnaeus, 1758).

#### Pectinoidea

- alessii*, *Pecten* – Philippi, 1836a: ix, 85; 1844g: 58. Enna, Sicily, Italy; fossil [Late Pliocene – Early Pleistocene]. *Flabellipecten alessii* (Philippi, 1836) (Glibert & Van de Poel, 1965b: 15; Jiménez et al., 2009: 15–17, fig. 6c, 6d).
- amiculus*, *Pecten* – Philippi, 1851c: 89. Madagascar. The Indian Ocean *Decatopecten amiculum* (Philippi, 1851) (Higo et al., 1999: 446; Okutani, 2000: 906–907, fig. 46; Dijkstra & Kilburn, 2001: 276–277, figs. 10–11; Raines & Poppe, 2006: 104–105, pl. 43, figs. 1–7, pl. 44, figs. 1–7, pl. 45, figs. 1–8, pl. 48, figs. 2, 7; Huber, 2010: 198). Type material not found (Dijkstra & Knudsen, 1998: 55).
- andinus*, *Pecten* – Philippi, 1899: 28, pl. 16, fig. 4. Cerro de Herrera, Colchagua, Chile; Guill. Krug; [Mesozoic]. Syntype, SGO.PI.893 (n = 1 valve). Synonym of "*Chlamys*" *textoria* (Schlotheim, 1820); Jurassic of Argentina and Chile (Damborenea, 2002b: 76).
- angustecostatus*, *Pecten* – Philippi, 1899: 27, pl. 16, fig. 1, pl. 14, fig. 2. San Poman, Amolanas, Chile; [Mesozoic]. Syntypes, SGO.PI.874 (n = 1 valve, figured on pl. 16, fig. 1); SGO.PI.875 (n = 1, figured on pl. 14, fig. 2). *Weyla alata angustecostata* (Philippi, 1899); Jurassic (Damborenea & Manceñido, 1979: 98; Damborenea, 2002b: fig. 2G, H). However, Aberhan (1994: 44) determined that this subspecies could not be differentiated from *W. alata* (Buch, 1838), "because of a continuous morphological spectrum with numerous intermediate specimens that cannot be attributed clearly to one of the two subspecies".
- angustus*, *Pecten* – Philippi, 1899: 27, pl. 16, fig. 3. Tinguiririca, Portezuelo, Chile; Fr. Albert; [Mesozoic]. Syntypes, SGO.PI.891 (n = 2 valves); SGO.PI.892 (n = 1 valve).
- antarticus* [sic], *Pecten* – Philippi, 1897: 370 ["*leguasi* var. ?"] East of Punta Pabellón, Isla Chiloé, Chile; [Cenozoic?]. The species name was probably intended to be "*antarcticus*."
- antiquatus*, *Pecten* – Philippi, 1844z4: 50; 1844g: 61, 300, pl. 16, fig. 5. Tertiary of Freden & Diekholtz, Niedersachsen, Germany



- [Late Oligocene]. Synonym of *Propeamusium pygmaeum* (Münster, 1835) (Janssen, 1979b: 47–48). The material he reported in 1844 from a Pliocene locality in Italy (Philippi, 1844g), is probably not the same species.
- antonii*, *Pecten* – Philippi, 1844f: 99 [1], pl. 1, fig. 1. Locality unknown. Synonym of *Pecten laqueatus* Sowerby, 1842, from the northwestern Pacific (Lischke, 1867: 180; Schrenck, 1867: 482–484).
- apolis*, *Pecten* “?” – Philippi, 1899: 37, pl. 20, fig. 11. Locality unknown, Chile; [Mesozoic].
- araucanus*, *Pecten* – Philippi, 1887a: 209 [1887b: 202], pl. 46, fig. 7. “Tumbez”, Chile; Francisco J. Ovalle & Isla Quiriquina; Cretaceous. Syntype, SGO.PI.207 (Hualpén, near Concepcion). Synonym of *Pecten granulatus* d’Orbigny, 1847 (Wilckens, 1904: 224), or of *Chlamys* (*Mixtipecten*) *chilensis* (d’Orbigny, 1846), Maastrichtian (Stinnesbeck, 1986: 170–172, pl. 2, figs. 8–13).
- aurantia*, *Pecten testae* var. – Philippi, 1836a: 81, as var. “aurantia”. Locality presumably Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1889: 112), as *Pecten incomparabilis* var. *aurantia* Philippi, 1836.
- australis*, *Pecten* – Philippi, 1845i: 56–57, non G. B. Sowerby II, 1842. Isla Chonos, Chile. *Pecten rosaceus* Stempell, 1899, a replacement name but was itself *non* Deshayes, 1863, and *non* Locard, 1888. *Pecten* (*Chlamys*) *amandi* Hertlein, 1935; replacement name. Roth (1975: 85, fig. 1) stated that the “holotype” of this species was in the Museo Nacional de Historia Natural, Santiago, but Dijkstra & Köhler (2008: 32) stated that “a holotype does not exist because the description is not explicitly based on a single specimen,” and that Roth’s act was not a valid lectotype designation, so that the MNHNS valves were “possible syntypes only” (not found in March 2014). Lectotype, ZMB 16193 (14.6 mm x 16.9 mm), designated by Dijkstra & Köhler (2008: 32–33, fig. 2b; previously figured by Waloszek, 1984: 218, 220, pl. 2, fig. 6 as “cotypus”). Synonym of *Psychrochlamys patagonica* (King, 1832) (Jonkers, 2003: 46; Raines & Poppe, 2006: 226, 342, pl. 173, figs. 1–4, pl. 174, figs. 1–6, as “King & Broderip”; Güller & Zelaya, 2016a: Supplementary Materials, at 4, as “*Zygochlamys*”).
- bernardi*, *Pecten* – Philippi, 1851c: 90. Locality unknown. Possible syntypes, ZMB 103076 (n = 3) (Dijkstra & Köhler, 2008: 33, 34, fig. 2c). The “holotype” (BMNH 1923.7.13.7) cited by Wagner (1989: 55, fig. 3) “is not a type of the taxon, as can be concluded from examination of the specimen, sales lists, and correspondence of the museum” (Dijkstra & Köhler, 2008: 35). *Cryptopecten bernardi* (Philippi, 1851) from French Polynesia (Higo et al., 1999: 445; Raines & Poppe, 2006: 312, pl. 275, figs. 1–7; Huber, 2010: 203).
- bisulcatus*, *Pecten* – Philippi, 1899: 28, pl. 16, fig. 7. Tinguiririca, Chile; C. Stolp; [Mesozoic]. Syntype, SGO.PI.896 (n = 1 valve).
- cardioides*, *Pecten* – Philippi, 1899: 29–30, pl. 17, fig. 2. Maricungam and Doña Ana, Chile; Peñon; [Mesozoic]. *Weyla cardioides* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98).
- cardiomorphus*, *Pecten* – Philippi, 1899: 30–31, pl. 17, fig. 5. Amolanas, Chile; G. A. Flühmann; [Mesozoic]. *Weyla cardiomorphus* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98).
- chiragra*, *Pecten* – Philippi, 1837d: 295–296, pl. 3, figs. 6, 7. Papantla, near Vera Cruz, Mexico; Tertiary.
- colchaguensis*, *Pecten* “?” – Philippi, 1899: 35, pl. 20, fig. 2. Cordillera de Tinguiririca, Chile; Mos. Amaral; [Mesozoic].
- commutatus*, *Pecten* – Philippi, 1899: 38, pl. 41, figs. 1, 2. Locality unknown, Chile; [Mesozoic]. *Weyla commutatus* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98); Jurassic. Aberhan (1994: 43) subsequently synonymized Philippi’s species with *Weyla alata* (Buch, 1838).
- compressus*, *Pecten* – Philippi, 1899: 38, pl. 41, figs. 3, 4. Juntas de Manflas, Chile; [Mesozoic]. *Weyla compressus* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98); Jurassic. Aberhan (1994: 43) subsequently synonymized Philippi’s species with *Weyla alata* (Buch, 1838).
- concolor*, *Pecten polymorphus* var. – Philippi, 1836a: 80, as var. “concolor, cinnabarinus ...” Locality presumably Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1889: 95), as *Pecten flexuosus* var. *concolor* Philippi, 1836.
- crebricostatus*, *Pecten* – Philippi, 1844f: 100 [2], pl. 1, fig. 2. China. Synonym of the Indo-Pacific *Minnivola pyxidata* (Born, 1778) (Eames & Cox, 1956: 28; Raines & Poppe, 2006: 172–173, 387, pl. 120, figs. 1, 4–7, pl. 121, figs. 1–7).



- curvicosta*, *Pecten* – Philippi, 1899: 31–32, pl. 18, fig. 3a, 3b. Cordillera de Tinguiririca, Chile; [Mesozoic]. Syntypes, SGO.PI.876 (n = 1 valve); SGO.PI.877 (n = 1 valve); SGO.PI.879 (n = 1 valve); SGO.PI.880 (n = 1). *Weyla curvicosta* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98); Jurassic. Subsequently, Aberhan (1994: 43) tentatively synonymized Philippi's species with *Weyla alata* (Buch, 1838).
- delicatulus*, *Pecten* – Philippi, 1887a: 209 [1887b: 201–202], pl. 46, fig. 5. Hualpen & Isla Quiriquina, Chile; Cretaceous. Syntypes, SGO.PI.206 (n = 1 valve, from Isla Quiriquina); SGO.PI.663 (n = 1 valve, Hualpen, labeled as “holotipo”). Synonym of *Pecten granulatus* d'Orbigny, 1846 (Wilckens, 1904: 224), or *Chlamys (Mixtipecten) chilensis* (d'Orbigny, 1846), Maastrichtian (Stinnesbeck, 1986: 170–172, pl. 2, figs. 8–13).
- deserti*, “*Pecten? Terebratula?*” – Philippi, 1860a: 145 [1860b: 128], Petref. pl. 1, fig. 9. Philippi was thus undecided as to the phylum of his specimen (Mollusca or Brachiopoda). Desierto de Atacama, Chile; [Mesozoic or Cenozoic?].
- dilatatus*, *Pecten* – Philippi, 1899: 30, pl. 17, fig. 4. “Destiladero” [Copaipó, Atacama], Chile; Paul. Ortega; [Mesozoic]. Syntype, SGO.PI.908 (n = 1 valve). *Weyla dilatatus* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98).
- discors*, *Pecten* – Philippi, 1899: 32–33, pl. 19, fig. 1, *non* Lamarck, 1819, *non* Borson, 1825. “Alto del Molle”, Chañarcillo, Chile; Pastor Soto; [Mesozoic].
- disculus*, *Pecten* – Philippi, 1899: 35–36, pl. 20, fig. 5. Locality unknown, Chile; Carlos Stolp; [Mesozoic]. Syntype, SGO.PI.904 (n = 1).
- domeykoi*, *Pecten* – Philippi, 1899: 24–25, pl. 13, fig. 4. Amolanas, Chile; Flühmann; [Mesozoic]. *Weyla domeykoi* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98).
- eurypterus*, *Pecten* – Philippi, 1899: 32, pl. 18, fig. 5. Portezuelo de Doña Ana, Chile; J. Domeyko; [Mesozoic].
- exasperata*, *Lima* – Philippi, 1899: 19, pl. 10, fig. 3. Andium de Peñon, Chile; A. Martinez; [Mesozoic]. Holotype, SGO.PI.941 (Damborenea, 2002b: 76, fig. 28e–f). “*Chlamys*” *textoria* (Schlotheim, 1820); Jurassic of Argentina and Chile (Damborenea, 2002b: 76–77).
- excavatus*, *Pecten* – Philippi, 1899: 31, pl. 18, fig. 1a, 1b, *non* Anton, 1838, *non* Valenciennes, 1846. “Tres Puntas” [Atacama], Chile; Ign. Domeyko; [Mesozoic]. Syntype, SGO.PI.886 (n = 1 valve). *Weyla excavatus* (Philippi, 1899), Jurassic (Damborenea & Manceñido, 1979: 98), but a new name would be needed for this junior primary homonym. Subsequently, Aberhan (1994: 43) tentatively synonymized Philippi's species with *Weyla alata* (Buch, 1838).
- fabricii*, *Pecten* – Philippi, 1844f: 101 [3], pl. 1, fig. 5. Greenland. Synonym of the North Atlantic-Arctic *Chlamys islandica* (O. F. Müller, 1776) (Higo et al., 1999: 441; Raines & Poppe, 2006: 184–185, 389, pl. 130, figs. 1–5, pl. 131, figs. 1–5, pl. 132, figs. 1–3).
- fimbriatus*, *Pecten* – Philippi, 1844g: 61, 300, pl. 16, fig. 6, *non* Phillips, 1836. Lamati, Calabria, Italy [Pliocene]. Dijkstra & Gofas (2004: 47) concluded that this species was based on a left valve, while the material he reported in 1844g (p. 61, pl. 16, fig. 5) as *Pecten antiquatus* Philippi, 1844, was based on the right valve of the same species. However, Dijkstra & Gofas, 2004: 45–47) assumed that Philippi's 1844 usage of *antiquatus* was an available description, when it was in fact an erroneous extension of an Oligocene species Philippi had described in 1844 to the Pliocene. They noted that type material was not found in Berlin. The name *Pecten fimbriatus* Philippi, although a junior primary homonym, is maintained under ICZN Code Article 23.9.1 (1999), now *Cyclopecten fimbriatus* (Dijkstra, pers. comm., May 2013). It was incorrectly listed as a synonym of *Pseudamussium clavatum* (Poli, 1795) by Raines & Poppe (2006: 78–79, 389).
- gayi*, *Pecten* – Philippi, 1887a: 211 [1887b: 204], pl. 45, fig. 8. Coquimbo “?”, Chile; Tertiary. Holotype, SGO.PI.223 (n = 1).
- glaphyrus*, *Pecten* – Philippi, 1899: 34–35, pl. 20, fig. 1. Doña Ana & Peñon, Chile; [Mesozoic]. Syntype, SGO.PI.910 (Damborenea, 2002b: 63, fig. 28d, as a species “of dubious validity”).
- goliath*, *Pecten* – Philippi, 1899: 26, pl. 14, fig. 1. Vallenar Andibus and Río Tinguiririca, Chile; [Mesozoic]. Syntypes, SGO.PI.873 (n = 1 valve, Vallenar); SGO.PI.5013 (n = 1 valve, Vallenar); SGO.PI.905 (n = 1 valve, Cordillera di Tinguiririca). *Weyla goliath* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98).
- harneckeri*, *Pecten* – Philippi, 1899: 32, pl. 18, fig. 4a, 4b. Caracoles [Antofagasta], Chile; O. Harnecker; [Mesozoic]. Syntype,



- SGO.PI.898 (n = 1 valve). *Weyla harnackeri* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98).
- heteroclines*, *Pecten* – Philippi, 1899: 29, pl. 16, fig. 8. Locality unknown, Chile; [Mesozoic]. Syntype, SGO.PI.911 (n = 1). “*Chlamys*” *textoria* (Schlotheim, 1820); Jurassic of Argentina and Chile (Damborenea, 2002b: 76).
- humilis*, *Pecten* – Philippi, 1899: 28, pl. 16, fig. 5. Portezuelo del Tinguiririca, Chile; Fr. Albert; [Mesozoic]. Syntypes, SGO.PI.903 (n = 1 valve; Damborenea, 2002b: 62, fig. 28b, erroneously listed as “holotype”); SGO.PI.902 (n = 2 valves). Damborenea (2002b: 62) noted that one of the type specimens (i.e., SGO.PI.903) “is not complete enough as to refer it with certainty to any pectinid species, but can be a young *P. tinguiriricanus*” (also described by Philippi, 1899) from the Jurassic.
- hupeanus*, *Pecten* – Philippi, 1887a: 211 [1887b: 203], pl. 47, fig. 4, *nom. nov. pro Pecten propinquus* Hupé, *non* Münster, 1833. SGO.PI.208, from Coquimbo, is labeled as the “holotipo”, but this is just Philippi’s figured specimen, not Hupé’s original type material. The Pliocene *Chlamys hupeanus* (Philippi, 1887) (Herm, 1969: 104–105, pl. 1, figs. 5, 6), or *Zygochlamys hupeanus* (Philippi, 1887) (Jonkers, 2003: 42, pl. 7, figs. d–f; Griffin & Nielsen, 2008: 281–283, pl. 14, fig. 4, who figured one of Hupé’s syntypes).
- insularis*, *Pecten* – Philippi, 1897: 369, pl. 7. East of Punta Pabellón, Isla Chiloé, Chile; [Cenozoic?].
- laeviusculus*, *Hinnites* – Philippi, 1844g: 62, 300, pl. 16, fig. 8. Calabria, Sicily, Italy; fossil. Synonym of *Hinnites crispa* (Brocchi, 1814).
- larenasi*, *Pecten* – Philippi, 1887a: 209–210 [1887b: 202], pl. 58, fig. 16. Tomé, Chile; Cretaceous. Synonym of *Pecten granulatus* d’Orbigny, 1846 (Wilckens, 1904: 224), or of *Chlamys (Mixtipecten) chilensis* (d’Orbigny, 1846), Maastrichtian (Stinnesbeck, 1986: 170–172, pl. 2, figs. 8–13).
- leguasi*, *Pecten* – Philippi, 1897: 369–370, pl. 8. East of Punta Pabellón, Isla Chiloé, Chile; [Cenozoic?].
- lycorrhynchus*, *Pecten* – Philippi, 1899: 29, pl. 17, fig. 1. Locality unknown, Chile; [Mesozoic]. Holotype, SGO.PI.887 (n = 1 valve). *Weyla lycorrhynchus* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98). Synonym of *Weyla (Lywea) unca* (Philippi, 1899); Jurassic (Damborenea, 1987b: 187–189, pl. 12, fig. 4, pl. 13, figs. 1–11, figs. 24–25; Aberhan, 1994: 46).
- martinezi*, *Pecten* – Philippi, 1899: 36–37, pl. 20, fig. 9. Peñon, Chile; Aristides Martinez. Holotype, SGO.PI.910 (n = 1 valve; Damborenea, 2002b: 76, fig. 28c). Synonym of “*Chlamys*” *textoria* (Schlotheim, 1820); Jurassic of Argentina and Chile (Damborenea, 2002b: 76–77).
- multistriatus*, *Pecten* – Philippi, 1837c: 286, *non* Deshayes, 1830 [*nomen nudum*].
- nannus*, *Pecten* – Philippi, 1899: 28, pl. 16, fig. 6. Portezuelo del Tinguiririca, Chile; Fr. Albert; [Mesozoic]. Syntypes, SGO.PI.882 (n = 1 valve); SGO.PI.883 (n = 1 valve); SGO.PI.884 (n = 1 valve); SGO.PI.885 (n = 1 valve).
- natans*, *Pecten* – Philippi, 1845i: 57. Messier Canal & Smith Canal, Strait of Magellan. Lectotype, ZMB 16262a (29.9 mm x 34.3 mm), designated by Jonkers (2003: 60); paralectotypes, ZMB 16262b–e (n = 4); additional possible paralectotypes, SMF 315296 (n = 3). *Austrochlamys natans* (Philippi, 1845) of Argentina and Chile (Jonkers, 2003: 60–61, pl. 2, figs. a, c, e, pl. 15, figs. a, b; Dijkstra & Köhler, 2008: 38–39, fig. 3c; Huber, 2010: 211; Rosenfeld et al., 2015: 80, fig. 7F; Güller & Zelaya, 2016a: 237); type species (OD) of *Austrochlamys* Jonkers, 2003. *Pecten “nasans”* of Reeve (1853) and later authors is in error (Bernard, 1983: 25; Waloszek, 1984: 229–230).
- oblongus*, *Pecten* – Philippi, 1844g: 300, pl. 16, fig. 7 [*non* Philippi, 1893b]. Lake Como, Italy; fossil. The Mio-Pliocene *Amusium (Korobkovia) oblongum* (Philippi, 1844) (Glibert & Van de Poel, 1965b: 11), or now *Korobkovia oblonga* (Philippi, 1844), Pliocene (Jiménez et al., 2009: 11–13, fig. 5e).
- oblongus*, *Pecten* – Philippi, 1893b: 13, pl. 2, fig. 4, ex Bravard ms, *non* Philippi, 1844g. Argentina; Tertiary. *Flabellipecten oblongus* (Philippi, 1893); late Miocene (del Río, 1991: 49–50, pl. 3, figs. 1, 2; del Río & Martínez, 1998: 56, pl. 18, fig. 5; Martínez & del Río, 2002: 178), or *Leopecten oblongus* (Philippi, 1893); Upper Miocene, Paraná Formation, Argentina (Waller, 2007: 937). Philippi’s 1893 name requires renaming because of the homonymy with his own 1844 name, *supra*.
- ovatus*, *Pecten* – Philippi, 1899: 27, pl. 16, fig. 2, *non* M’Coy in Griffith, 1844. Locality unknown, Chile; Carlos Stolp; [Mesozoic].
- oxyrrhynchus*, *Pecten* – Philippi, 1899: 31, pl. 18, fig. 2. “Totoralillo” [Atacama], Chile;



- Ign. Domeyko; [Mesozoic]. Syntype, SGO. Pl.889 (n = 1 valve). *Weyla oxyrrhynchus* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98).
- paragodus*, *Pecten* – Philippi, 1899: 25, pl. 13, fig. 5. Chañarcillo, Chile; [Mesozoic]. *Weyla paragodus* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98).
- parvulus*, *Pecten* – Philippi, 1887a: 212 [1887b: 204], pl. 46, fig. 2. Navidad, Chile; Tertiary [Miocene].
- pencanus*, *Pecten* – Philippi, 1887a: 209 [1887b: 202], pl. 58, fig. 5. Hualpen, Chile; Cretaceous. Syntypes, SGO.Pl.664 (n = 2 valves, labeled as “paralectotipo”). Synonym of *Pecten granulatus* d’Orbigny, 1846 (Wilckens, 1904: 224), or of *Chlamys* (*Mixtipecten*) *chilensis* (d’Orbigny, 1846), Maastrichtian (Stinnesbeck, 1986: 170–172, pl. 2, figs. 8–13).
- pleuronectoides*, *Pecten* – Philippi, 1899: 37 [Jurassic, Chile]. Published in synonymy of *Pecten paradoxus* Münster in Goldfuss, 1838.
- problematicus*, *Pecten* “?” – Philippi, 1899: 25–26, pl. 13, fig. 2. Cordillera de Tinguiririca, Chile; [Mesozoic]. Syntypes, SGO.Pl.901 (n = 1 valve).
- remondi*, *Pecten* – Philippi, 1887a: 211 [1887b: 204], pl. 45, fig. 6. Coquimbo, Chile; A. Rémond; Tertiary. Syntype, SGO.Pl.222 (n = 1 valve). *Chlamys vidali* (Philippi, 1887) (Herm, 1969: 103–104).
- rimulosus*, *Pecten* – Philippi, 1844g: 60–61, 300, pl. 16, fig. 4; 1844z3: 3, 4. Pezzo, Calabria, & Messina, Italy. Synonym of *Palliolium striatum* (O. F. Müller, 1776) (Sabelli et al., 1990: 290; Raines & Poppe, 2006: 72–73, 398, pl. 5, figs. 4–9).
- simpsoni*, *Pecten* – Philippi, 1887a: 210 [1887b: 202–203], pl. 46, fig. 1. Ranquil, Isla Chiloe (Enrique Simpson & Karl Martin); Huiñimo (Wenceslao Diaz), Isla La Mocha, Navidad; all Chile; Tertiary. Syntypes, SGO. Pl.210 (n = 1, Chiloe); SGO.Pl.211 (n = 1 valve, Ranquil); SGO.Pl.213 (n = 1, Navidad); SGO.Pl.659 (n = 2 valves, Isla La Mocha). *Chlamys simpsoni* (Philippi, 1887); Pliocene (Herm, 1969: 102–103, pl. 2, figs. 1, 2, pl. 4, fig. 6); Miocene (DeVries & Frassinetti, 2003: 125; Frassinetti, 2006: 64, figs. 3, 4).
- stolpi*, *Pecten* – Philippi, 1899: 34, pl. 19, fig. 5. Valle del Tinguiririca, Chile; [Mesozoic]. Syntype, SGO.Pl.897 (n = 1). *Weyla stolpi* (Philippi, 1899), Jurassic (Damborenea & Manceñido, 1979: 98). Aberhan (1994: 43) subsequently synonymized Philippi’s species with *Weyla alata* (Buch, 1838).
- subcarinatus*, *Pecten* – Philippi, 1899: 34, pl. 19, fig. 4a, 4b. Locality unknown, Chile; [Mesozoic]. *Weyla subcarinatus* (Philippi, 1899), Jurassic (Damborenea & Manceñido, 1979: 98). Aberhan (1994: 43) subsequently synonymized Philippi’s species with *Weyla alata* (Buch, 1838).
- sulfurea*, *Pecten testae* var. – Philippi, 1836a: 81, as var. “sulfurea”. Locality presumably Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1889: 112), as *Pecten incomparabilis* var. *sulfurea* Philippi, 1836.
- sundti*, *Pecten* – Philippi, 1899: 35, pl. 20, fig. 4. Chaco, Deserto de Atacama, Chile; Lorenz Sundt; [Mesozoic]. Syntype, SGO. Pl.906 (n = 1).
- tenuistriatus*, *Pecten* – Philippi, 1899: 36, pl. 20, fig. 6, non Münster, 1833. Doña Ana, [Coquimbo], Chile; Frid. Philippi & Ign. Domeyko; [Mesozoic]. Syntypes, SGO.Pl.895 (n = 1); SGO.Pl.5027 (n = 1).
- testae*, *Pecten* – Philippi, 1836a: ix, 81, pl. 5, fig. 17, 17a, ex Bivona ms.; 1844g: 57. Palermo & Tripani, Sicily, Italy. Synonym of *Palliolium incomparabile* (Risso, 1826) (Sabelli et al., 1990: 291).
- textus*, *Pecten* – Philippi, 1844z4: 50, 72, [87], pl. 2, fig. 16. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. Synonym of *Palliolium decussatum* (Münster in Goldfuss, 1833) (Rust, 1999: 37; R. Janssen, pers. comm., April 2013).
- tinguiriricanus*, *Pecten* – Philippi, 1899: 36, pl. 20, fig. 8. Tinguiririca, Chile; Car. Stolp; [Mesozoic]. Damborenea (2002b: 62, fig. 28a) stated that SGO.Pl.907 was the “holotype”, but she noted that its label stated that it came from “Sasneado” (not from Tinguiririca), which she thought was probably an error for Sosneado, Argentina, and then incorrectly concluded that this species may be a senior synonym of the Jurassic *Radulonectites sosneadoensis* (Weaver, 1931), from the same locality. However, there is no basis to conclude that SGO.Pl.907 is actually the type specimen; it is equally possible that the original type specimen, from Tinguiririca, is now lost.
- tunica*, *Pecten* – Philippi, 1844f: 100–101 [2–3], pl. 1, fig. 3. “Hawaii”; E. B. Philippi. Mislocalized and a junior synonym of the northeastern Pacific *Leptopecten latiauratus* (Conrad,



- 1837) (Bernard, 1983: 25; Raines & Poppe, 2006: 322–323, 401, pl. 282, figs. 1–8).  
*uncus, Pecten* – Philippi, 1899: 30, pl. 17, fig. 3. Amolanas, Atacama, Chile; Gust. Ad. Flühmann; Jurassic. Type species (OD) of *Lywea Damborenea*, 1987. Lectotype, SGO.PI.909, designated by Damborenea (1987b: 188, fig. 25–1); Jurassic, Chile & Argentina. *Weyla (Lywea) unca* (Philippi, 1899) (Damborenea & Manceñido, 1979: 98; Damborenea, 1987b: 187–189, pl. 12, fig. 4, pl. 13, figs. 1–11, figs. 24, 25; Aberhan, 1994: 46, pl. 23, fig. 5, pl. 24, fig. 2, pl. 25, fig. 2).  
*vidali, Pecten* – Philippi, 1887a: 212 [1887b: 204–205], pl. 47, fig. 5. Mejillones del Sur, Chile; Ramón Vidal Gormáz; Quaternary. Syntype, SGO.PI.656 (n = 1). The Pliocene *Chlamys vidali* (Philippi, 1887) (Herm, 1969: 103–104, pl. 1, figs. 1, 2; DeVries & Frassinetti, 2003: 126); or *Zygochlamys vidali* (Philippi, 1887) (Jonkers, 2003: 41–42, pl. 7, figs. 4a–4c).  
*villaroeli, Pecten* – Philippi, 1899: 36, pl. 20, fig. 7. Caracoles [Antofagasta]; Villaroel & Cajon del Dorazno [Colchagua]; Fried. Abert; [Mesozoic]. Syntypes, SGO.PI.899 (n = 1, Caracoles); SGO.PI.935 (n = 1 valve, Cajon del Dorazno); SGO.PI.5030 (n = 1 valve, Caracoles).

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- “*aspersus, Pecten*” – Philippi, 1844g: 57. This was listed by Sabelli et al. (1990: 290) as if it were a new, homonymous species by Philippi, but it was merely his misuse of *Pecten aspersus* Lamarck, 1819.  
“*gibbus, Pecten*” – Philippi, 1836a: 83–84. Listed by Sabelli et al. (1990: 289) as if it were a new, homonymous species by Philippi, but it was merely his misuse of *Pecten gibbus* Lamarck, 1819.  
“*hyalinus, Pecten*” – Philippi, 1836a: ix, 80–81. As “mihi” for a transfer of *Ostrea hyalina* Poli, 1795, to *Pecten*.  
“*porphyreus, Pecten*” – Philippi, 1844f: 101–102 [3–4]. Listed by Sherborn (1929: 5116) as if it were a name by Philippi, but this Chemnitz name was first made available as *Ostrea porphyrea* Gmelin, 1791.

#### Spondylidae

- buchi, Spondylus* – Philippi, 1845z: 449 [*nomen nudum*]; 1847-l: 55, pl. 7, fig. 9a, b. Osterweddingen & Wolmirsleben, Sachsen-Anhalt, Germany; Late Eocene/Early Oligo-

cene. Syntypes, PHB MB M.\_\_\_\_ (H) 4 (n = 3 valves) (largest valve 44.0 mm x 40.0 mm). *Spondylus buchi* (Philippi, 1847) (Koenen, 1893: 1036–1039, pl. 66, figs. 1–4).

#### Plicatulidae

- caracolensis, Plicatula* – Philippi, 1899: 22–23, pl. 12, fig. 5. Caracoles [Antofagasta], Chile; W. Diaz; [Mesozoic]. Syntype, SGO.PI.918 (n = 1 valve).  
*mytilina, Plicatula* – Philippi, 1836a: ix, 86, pl. 6, fig. 1; 1844g: 62. Palermo, Sicily, Italy; Miocene. Syntype, PHB MB M.\_\_\_\_ (H) 14 (n = 1 valve) (8.3 mm x 9.8 mm). *Plicatula mytilina* Philippi, 1836 (Lozouet et al., 2003: 6, pl. 14, figs. 1–6).  
*regularis, Plicatula* – Philippi, 1849s: 31–32. Formosa; Cécille via Largilliert. The western Pacific *Plicatula regularis* Philippi, 1849 (Huber, 2010: 193, 622).

#### Limidae

- aconcaguina, Lima* – Philippi, 1899: 21–22, pl. 11, fig. 7. Melon, Chile; [Mesozoic].  
*chilense, Ctenostreon* – Philippi, 1899: 23, pl. 12, figs. 1–3. Portezuelo, Tinguiririca valley, and Cerro de Herrera [Colchagua], Chile; [Mesozoic]. Syntypes, SGO.PI.916 (n = 1 valve, specimen in fig. 2, from Portezuelo); SGO.PI.917 (n = 1 valve, specimen in fig. 3, from Cerro de Herrera).  
*decemcostata, Lima* “?” – Philippi, 1899: 22, pl. 11, fig. 9. Tres Cruces de Paihuano, [Coquimbo], Chile; [Mesozoic]. Syntype, SGO.PI.943 (n = 1 valve).  
*discors, Lima* “?” – Philippi, 1899: 20–21, pl. 11, fig. 4. Caracoles “?”, Atacama; Ern. Williams; [Mesozoic]. Syntype, SGO.PI.5014 (n = 1).  
*hupei, Lima* “?” – Philippi, 1899: 19, pl. 10, fig. 4. Locality unknown, Chile; H. Volckmann; [Mesozoic].  
*perobliqua, Lima* – Philippi, 1899: 22, pl. 11, fig. 8. Cordillera de Doña Ana, Chile; Federico Philippi; [Mesozoic].  
*pygmaea, Lima* – Philippi, 1845i: 56. Strait of Magellan. *Limatula (Squamilima) pygmaea* (Philippi, 1845) (Dell, 1964: 182–183, pl. 2, fig. 13; 1990: 55; Fleming, 1978: 28, 82, fig. 98; Narchi et al., 2002: 659–661, fig. 23), or *Limatula pygmaea* (Philippi, 1845) (Bernard, 1983: 22; Aldea & Troncoso, 2008: 96–97, fig. 95), or *Limea (Gemellima) pygmaea* (Philippi, 1845) (Huber, 2010: 639; Güller & Zelaya, 2016a: 237).



*radula*, Lima – Philippi, 1899: 20, pl. 11, fig. 2. Andes de Vallenar, Chile; J. M. Reyes; [Mesozoic]. Syntype, SGO.PI.939 (n = 1).

*ranquelensis*, Lima – Philippi, 1899: 20, pl. 11, fig. 3. Sadneado, E. side of Cordillera de San Fernando [Colchagua], Chile; [Mesozoic]. Syntype, SGO.PI.942 (n = 1 valve).

*sacki*, Lima – Philippi, 1845z: 449 [*nomen nudum*]; 1847-l: 54, pl. 7, fig. 10a–c. No locality; Sack's collection. The Upper Eocene *Limatula* (*Gemellima*) *sacki* (Philippi, 1847) (Glibert & Van de Poel, 1965b: 49, as "1846").

#### Trigonoidea s.l.

*Anopisthodon* – Philippi, 1899: 74. Type species (M): *Trigonia obesa* Philippi, 1899. Mesozoic; Chile. *Nomen dubium* (Cox, 1969c: N489).

*Aulacopleurum* – Philippi, 1899: 94. Type species (SD Cox, 1969): *Trigonia* "??" *trapezoidea* Philippi, 1899. Mesozoic; Chile. *Nomen dubium* (Cox, 1969c: N489).

*aequilatera*, *Trigonia* – Philippi, 1899: 74, pl. 33, fig. 4, 4a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 26). *Trigonia* (?) *aequilatera* Philippi, 1899.

*amarali*, *Trigonia* – Philippi, 1899: 67, pl. 30, fig. 6. Valle de Tinguiririca, Chile; Mose Amaral; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 22). *Steinmannella* (S.) *amarali* (Philippi, 1899).

*angusta*, *Trigonia* – Philippi, 1899: 79–80, pl. 35, figs. 1, 2. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Lectotype, SGO.PI.3129 (n = 1 valve), designated by Pérez & Reyes (1983: 18, pl. 1, figs. 11, 12 & 15). *Anditrigonia eximia* (Philippi, 1899) (Pérez & Reyes, 1983: 16–22, pls. 1–3; 1989: 15, pl. 2, figs. 5, 9).

*arsinoe*, *Trigonia* – Philippi, 1899: 76, pl. 34, fig. 2. Junta de Manflas, Copiapó, Chile; Volckmann; [Mesozoic]. Lectotype, SGO.PI.3125 (n = 1 valve), designated by Pérez & Reyes (1983: 17, pl. 1, figs. 4 & 8). *Anditrigonia eximia* (Philippi, 1899) (Pérez & Reyes, 1983: 16–22, pls. 1–3; 1989: 13, pl. 2, fig. 13).

*baccifera*, *Trigonia* – Philippi, 1899: 83–84, pl. 36, fig. 1, 1a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Lectotype, SGO.PI.3136 (n = 1 valve), designated by Pérez & Reyes (1989: 12, pl. 1, figs. 6, 7, 9). *Pterotrigonia* (P.) *baccifera* (Philippi, 1899), or *Rinetrigonia baccifera* (Philippi, 1899) (Cooper, 2015: 16).

*baylei*, *Trigonia* – Philippi, 1899: 86–87, pl. 36, fig. 9. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Holotype, SGO.PI.3142 (n = 1 valve) (Pérez & Reyes, 1989: 13, pl. 2, figs. 12, 16). *Pterotrigonia* (P.) *baylei* (Philippi, 1899), or *Notoscabrotrigonia baylei* (Philippi, 1899) (Cooper, 2015: 25, 27).

*calderoni*, *Trigonia* – Philippi, 1899: 65, pl. 29, fig. 9. Valle de Tinguiririca, Chile; [Mesozoic]. Holotype, SGO.PI.3114 (n = 1 valve) (Río Tinguiririca, San Fernando, Chile) (Pérez & Reyes, 1989: 11, pl. 1, fig. 1). *Pterotrigonia* (?) *calderoni* (Philippi, 1899), but Philippi's name is a junior secondary homonym of *Trigonia calderoni* (del Castillo & Aguilera, 1895), from the Jurassic of Mexico. Cooper (2015: 21) stated that Philippi's species was "based on generically-indeterminate internal moulds and thus *nomina dubia*."

*consanguinea*, *Trigonia* – Philippi, 1899: 79, pl. 34, fig. 9, 9a. Río Tinguiririca, San Fernando, Chile; Moses Amaral; [Mesozoic]. Pérez & Reyes (1983: 17, pl. 1, figs. 14 & 18) stated that SGO.PI."3125" was the lectotype of this species, but that lot is actually the lectotype of *Trigonia arsinoe* Philippi, 1899; the type material of *T. consanguinea* was not found in February 2014. *Anditrigonia eximia* (Philippi, 1899) (Pérez & Reyes, 1983: 16–22, pls. 1–3; 1989: 25).

*copiapina*, *Trigonia* – Philippi, 1899: 71, pl. 32, fig. 1. Juntas de Manflas, Copiapó, Chile; Herm. Volckmann; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 22). *Steinmannella* (S.) *copiapina* (Philippi, 1899).

*coquandi*, *Trigonia* – Philippi, 1899: 84, pl. 36, fig. 3, 3a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Holotype, SGO.PI.3138 (n = 1 valve) (Pérez & Reyes, 1989: 12, pl. 1, figs. 8, 12). *Pterotrigonia* (P.) *coquandi* (Philippi, 1899), but Cooper (2015: 21) stated that Philippi's species was "based on generically indeterminate internal moulds and thus *nomina dubia*."

*cornuta*, *Trigonia* – Philippi, 1899: 75, pl. 33, fig. 6, 6a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 26). *Trigonia* (?) *cornuta* Philippi, 1899.

*crassidens*, *Trigonia* – Philippi, 1899: 73, pl. 33, fig. 1, 1a, 1b. Tres Cruces de Paihuano, Vicuña, Chile; [Mesozoic]. Lectotype, specimen illustrated by Philippi, designated by Pérez & Reyes (1983: 17, pl. 1, fig. 22) (not found in February 2014). *Anditrigonia eximia* (Philippi, 1899) (Pérez & Reyes, 1983: 16–22, pls. 1–3; 1989: 24).



- discors*, *Trigonia* – Philippi, 1899: 75–76, pl. 34, fig. 1, 1a. Cajon de la Leña, Cauquenes, Cancagua, Chile; Pastore Soto & Valle de Tinguiririca; [Mesozoic]. Neotype, SNGM-7007 (IIG 103), the paratype of *Trigonia eximia* var. *multicostata* Corvalán, 1959, a junior synonym of Philippi's species, designated by Pérez & Reyes (1983: 22–23, pl. 4, fig. 7). *Anditrigonia discors* (Philippi, 1899) (Pérez & Reyes, 1983: 22–26, pl. 4; 1989: 24).
- domeykoana*, *Trigonia* – Philippi, 1860a: 144 [1860b: 126–127], Petref. pl. 1, figs. 5, 6, 1899: 74, pl. 33, fig. 3, 3a, 3b. Desierto de Atacama, Chile; [Mesozoic or Cenozoic?]. Lectotype, SGO.PI.3122 (n = 1 valve) (Chaco, Taltal, Chile), designated by Pérez & Reyes (1989: 17, pl. 3, figs. 14, 16). *Trigonia* (?) *domeykoana* Philippi, 1860; Pérez & Reyes (1989) compared this with *Myophorella hillebrandti* Reyes & Pérez, 1985.
- erycina*, *Trigonia* – Philippi, 1899: 66, pl. 30, figs. 3, 3a, 5, 5a. Valle de Tinguiririca, Chile. Lectotype, SGO.PI.3115 (n = 1 valve) (Río Tinguiririca, San Fernando, Chile), designated by Pérez & Reyes (1989: 9–10, pl. 1, figs. 5, 10). *Steinmannella* (S.) *erycina* (Philippi, 1899) Tithonian, Upper Jurassic (Leanza & Garate Zubillaga, 1987: 217, pl. 13, fig. 7; Leanza, 1993: 44, pl. 7, fig. 1; Lazo, 2003: 1079, 1082).
- eudora*, *Trigonia* – Philippi, 1899: 83, pl. 35, fig. 12. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Holotype, SGO.PI.3135 (n = 1 valve) (Pérez & Reyes, 1989: 11–12, pl. 1, fig. 13). *Pterotrigonia* (P.) *eudora* (Philippi, 1899), but Cooper (2015: 21) stated that Philippi's species was “based on generically indeterminate internal moulds and thus *nomina dubia*.”
- eximia*, *Trigonia* – Philippi, 1899: 76–77, pl. 34, fig. 3, 3a, 3b. Valle de Tinguiririca, San Fernando, & Junta de Manflas, Copiapó, Chile; Volckmann. Lectotype, SGO.PI.3126 (n = 1 valve) (Río Tinguiririca, San Fernando, Chile), designated by Pérez & Reyes (1983: 17, pls. 2, figs. 3, 5, 7 & 8). *Anditrigonia eximia* (Philippi, 1899), Tithonian, Jurassic (Pérez & Reyes, 1983: 16–22, pls. 1–3; 1989: 13–14, pl. 2, figs. 7, 11, 14, 15; Leanza & Garate Zubillaga, 1987: 221–222, pl. 9, fig. 1; Leanza, 1993: 48–49, pl. 9, figs. 3–4).
- falciformis*, *Trigonia* “?” – Philippi, 1899: 83, pl. 35, fig. 11. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Holotype, SGO.PI.3134 (n = 1 valve) (Pérez & Reyes, 1989: 11, pl. 1, fig. 14). *Pterotrigonia* (?) *falciformis* (Philippi, 1899), but Cooper (2015: 21) stated that Philippi's species was “based on generically indeterminate internal moulds and thus *nomina dubia*.”
- fluehmanni*, *Trigonia* – Philippi, 1899: 69, pl. 31, fig. 4, as “*T. flühmanni*”. Alolanas, Copiapó, Chile; Gustavus Flühmann; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 21). *Trigonia* (T.) *fluehmanni* Philippi, 1899.
- foveata*, *Trigonia* – Philippi, 1899: 80, pl. 35, fig. 3, 3a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Lectotype, SGO.PI.3130 (n = 1), designated by Pérez & Reyes (1983: 18, pl. 1, figs. 2, 3, 13, 17). Synonym of *Anditrigonia eximia* (Philippi, 1899) (Pérez & Reyes, 1983: 16–22, pls. 1–3; 1989: 15, pl. 3, figs. 1, 2).
- gampsorrhyncha*, *Trigonia* – Philippi, 1899: 79, pl. 34, fig. 10. Río Tinguiririca, San Fernando, Chile; Moses Amaral; [Mesozoic]. Lectotype, SGO.PI.3128 (n = 1), designated by Pérez & Reyes (1983: 17–18, pl. 1, figs. 9, 10, 19, 21). Synonym of *Anditrigonia eximia* (Philippi, 1899) (Pérez & Reyes, 1983: 16–22, pls. 1–3; 1989: 14, pl. 2, fig. 1).
- glabra*, *Trigonia* “?” – Philippi, 1887a: 200 [1887b: 193], pl. 42, fig. 4, 4a, 4b. Isla Quiriquina & San Vicente, Chile; Cretaceous. Syntypes, SGO.PI.273 (n = 1, figured specimen, from Quiriquina), SGO.PI.278 (n = 1 valve, from San Vicente). *Sphenotrigonia* (?) *glabra* (Philippi, 1887) (Pérez & Reyes, 1989: 15–16, pl. 3, figs. 7, 10, who erroneously stated that the syntypes were the holotype and the paratype).
- glaphyra*, *Trigonia* – Philippi, 1899: 86, pl. 36, fig. 7. Río Tinguiririca, San Fernando, & Cerro de Herrera, Chile; Guill. Krug; [Mesozoic]. Syntype, SGO.PI.3140 (n = 1 valve) (Río Tinguiririca, San Fernando) (Pérez & Reyes, 1989: 12, pl. 2, figs. 3, 4, erroneously stated that this was the “holotype”). *Pterotrigonia* (P.) *glaphyra* (Philippi, 1899), or *Rinetrigonia glaphyra* (Philippi, 1899) (Cooper, 2015: 16).
- halimede*, *Trigonia* – Philippi, 1899: 91, pl. 38, fig. 5. Río Tinguiririca, San Fernando, Chile; Carlos Stolp; [Mesozoic]. Holotype, SGO.PI.3151 (n = 1 valve) (Pérez & Reyes, 1989: 18, pl. 5, fig. 3). *Trigonia halimede* Philippi, 1899.
- irregularis*, *Trigonia erycina* – Philippi, 1899: 66–67, pl. 32, fig. 3. Portezuelo Tinguiririca, San Fernando, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 22). Synonym of *Steinmannella* (S.) *erycina* (Philippi, 1899).
- lepida*, *Trigonia* – Philippi, 1899: 67, pl. 30, fig. 4. Valle de Tinguiririca, Chile; [Mesozoic]. Holotype, SGO.PI.3116 (n = 1 valve) (Río



- Tinguiririca, San Fernando, Chile) (Pérez & Reyes, 1989: 10, pl. 1, fig. 11). *Steinmannella* (S.) *lepida* (Philippi, 1899).
- leucothea*, *Trigonia* – Philippi, 1899: 77–78, pl. 34, fig. 6, 6a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Lectotype, SGO.PI.3127 (n = 1 valve), designated by Perez & Reyes (1983: 23, pl. 4, fig. 1). Synonym of *Anditrigonia discors* (Philippi, 1899) (Perez & Reyes, 1983: 22–26, pl. 4; 1989: 14, pl. 3, figs. 3, 4).
- macrorrhyncha*, *Trigonia* – Philippi, 1899: 77, pl. 34, fig. 5, 5a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Lectotype, specimen illustrated by Philippi, designated by Perez & Reyes (1983: 17, pl. 1, figs. 16, 20) (not found in February 2014). Synonym of *Anditrigonia eximia* (Philippi, 1899) (Perez & Reyes, 1983: 16–22, pls. 1–3; 1989: 25).
- manflarum*, *Trigonia* – Philippi, 1899: 77, pl. 34, fig. 4. Neica, Valle de Manflas, Copiapó & Cerro de Padre, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 23). *Vaugonia* (?) *manflarum* (Philippi, 1899).
- micippe*, *Trigonia* – Philippi, 1899: 71, pl. 31, fig. 8. Valle de Tinguiririca, Chile; [Mesozoic]. Lectotype, SGO.PI.3115 (n = 1 valve) (Río Tinguiririca, San Fernando, Chile), designated by Pérez & Reyes (1989: 7, 9, pl. 1, fig. 4); 1 paralectotype, SGO.PI.3115-1 (n = 1 valve). *Trigonia* (T.) *micippe* Philippi, 1899.
- nana*, *Trigonia* – Philippi, 1899: 85–86, pl. 36, fig. 6. Cerro del Padre, Manflas, Copiapó, Chile; Ramón Neira; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 26–27). *Trigonia* (?) *nana* Philippi, 1899.
- nereis*, *Trigonia* – Philippi, 1899: 70, pl. 31, fig. 6. Valle de Tinguiririca, Chile; Frid, Albert; [Mesozoic]. Holotype, SGO.PI.3118 (n = 1 valve) (Río Tinguiririca, San Fernando, Chile) (Pérez & Reyes, 1989: 7, pl. 1, fig. 2). *Trigonia* (T.) *nereis* Philippi, 1899.
- nux*, *Trigonia* – Philippi, 1899: 67–68, pl. 30, fig. 7. Valle de Tinguiririca, San Fernando, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 25–26). *Trigonia* (?) *nux* Philippi, 1899.
- obesa*, *Trigonia* “?” – Philippi, 1899: 74–75, pl. 33, fig. 5, 5a, 5b. Río Tinguiririca, San Fernando, Chile; Jurassic. *Nomen dubium* (Cox, 1969c: N489). Holotype, SGO.PI.3124 (Pérez & Reyes, 1989: 17, pl. 4, figs. 5, 6, 9). Although Pérez & Reyes (1989) were able to study the holotype, they agreed with Cox (1969c) that because the holotype is a poorly preserved, indeterminate internal mold, the species and the genus-level taxon *Anopisthodon* are *nomina dubia*.
- oreas*, *Trigonia* – Philippi, 1899: 91, pl. 38, fig. 4, 4a. Río Tinguiririca, San Fernando, Chile; Frid. Albert; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 27). *Trigonia* (?) *oreas* Philippi, 1899.
- ovalis*, *Trigonia* – Philippi, 1899: 65, pl. 29, fig. 8. Valle de Tinguiririca, Chile; [Mesozoic]. Holotype, SGO.PI.3113 (n = 1 valve) (Río Tinguiririca, San Fernando, Chile) (Pérez & Reyes, 1989: 11, pl. 2, figs. 6, 8). *Pterotrigonia* (?) *ovalis* (Philippi, 1899).
- ovallei*, *Trigonia* – Philippi, 1899: 78, pl. 34, fig. 8, 8a. Caracoles, Calama, Chile; Francisco Naveirio Ovalle & Arturo Villarroel; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 23). *Vaugonia* (V.) *ovallei* (Philippi, 1899).
- plagia*, *Trigonia* “?” – Philippi, 1899: 92, pl. 38, fig. 7, 7a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 27). *Trigonia* (?) *plagia* Philippi, 1899.
- pusilla*, *Trigonia* – Philippi, 1899: 78, pl. 34, fig. 7. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Lectotype, specimen illustrated by Philippi, designated by Perez & Reyes (1983: 17, pl. 1, fig. 1) (not found in February 2014). Synonym of *Anditrigonia eximia* (Philippi, 1899) (Perez & Reyes, 1983: 16–22, pls. 1–3; 1989: 25).
- rugosa*, *Trigonia* “?” – Philippi, 1899: 94, pl. 38, fig. 13, 13a. Portezuelo del Tinguiririca, San Fernando, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 27–28). *Trigonia* (?) *rugosa* Philippi, 1899.
- semicostata*, *Trigonia* – Philippi, 1899: 82, pl. 35, fig. 7. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Lectotype, SGO.PI.3133 (n = 1 valve), designated by Perez & Reyes (1983: 18, pl. 1, figs. 5–7). Synonym of *Anditrigonia eximia* (Philippi, 1899) (Perez & Reyes, 1983: 16–22, pls. 1–3; 1989: 15, pl. 3, figs. 5, 6).
- semilunata*, *Trigonia* – Philippi, 1899: 86, pl. 36, fig. 8, 8a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Lectotype, SGO.PI.3141 (n = 1 valve), designated by Pérez & Reyes (1989: 11–12, pl. 2, fig. 2). *Pterotrigonia* (P.) *semilunata* (Philippi, 1899), but Cooper (2015: 21) stated that Philippi’s species was “based on generically indeterminate internal moulds and thus *nomina dubia*.”
- steinmanni*, *Trigonia* – Philippi, 1899: 64, pl. 30, figs. 1, 2. Chilean Andes, Chile; Roberto



- Pizarro [Cretaceous]. Type material not found (Pérez & Reyes, 1989: 21). *Steinmannella steinmanni* (Philippi, 1899) (Leanza & Garate Zubillaga, 1987: 216–217, pl. 13, figs. 1–2; Leanza, 1993: 42–43, pl. 13, figs. 1–10; Lazo, 2003: 1079, 1082; Luci & Lazo, 2012: 106, 108). Type locality probably in the Valanginian de Punta Curaco, Pehuenchas, Argentina (Pérez & Reyes, 1989: 21).
- stolpi*, *Trigonia* – Philippi, 1899: 81–82, pl. 35, fig. 6. Río Tinguiririca, San Fernando, Chile; Carlos Stolp; [Mesozoic]. Holotype, SGO.PI.3132 (n = 1 valve) (Pérez & Reyes, 1989: 17, pl. 4, figs. 3, 4). *Trigonia stolpi* Philippi, 1899.
- sulcifera*, *Trigonia* – Philippi, 1899: 80–81, pl. 35, fig. 5. Portezuelo Tinguiririca, San Fernando, Chile; [Mesozoic]. Holotype, SGO.PI.3131 (n = 1 valve) (Pérez & Reyes, 1989: 9, pl. 1, fig. 3). *Trigonia (T.) sulcifera* Philippi, 1899.
- sundti*, *Trigonia* – Philippi, 1899: 69–70, pl. 31, fig. 5. Chaco, Taltal, Chile; Laurentius Sundt; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 26). *Trigonia (?) sundti* Philippi, 1899.
- tenuis*, *Trigonia* “?” – Philippi, 1899: 94–95, pl. 38, fig. 14. Portezuelo del Tinguiririca, San Fernando, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 28). *Trigonia (?) tenuis* Philippi, 1899.
- tenuistriata*, *Trigonia* – Philippi, 1899: 80, pl. 35, fig. 4. Junta de Manflas, Copiapó, Chile; Volckmann; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 26). *Trigonia (?) tenuistriata* Philippi, 1899.
- thetis*, *Trigonia* – Philippi, 1899: 71–72, pl. 32, fig. 2. Locality not stated, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 21). *Trigonia (T.) thetis* Philippi, 1899.
- trapezoidea*, *Trigonia* “?” – Philippi, 1899: 94, pl. 38, fig. 12. Portezuelo del Tinguiririca, San Fernando, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 27). *Nomen dubium* (Cox, 1969c: N489). Thus, the genus *Aulacopleurum* Philippi, 1899, based on this species is also a *nomen dubium*.
- triangularis*, *Trigonia* – Philippi, 1899: 88, pl. 37, fig. 5. Portezuelo del Tinguiririca, San Fernando, Chile; [Mesozoic]. Holotype, SGO.PI.3146 (n = 1 valve) (Pérez & Reyes, 1989: 17–18, pl. 4, fig. 8). *Trigonia triangularis* Philippi, 1899.
- tuberosa*, *Trigonia* – Philippi, 1899: 82, pl. 35, fig. 8. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 23). *Pterotrigonia (?) tuberosa* (Philippi, 1899); Tithonian, Jurassic (Kelly, 1995: 77).
- undulata*, *Trigonia* – Philippi, 1899: 70, pl. 31, fig. 7, *non* Fromherz in Agassiz, 1840. Valle de Tinguiririca, Chile; [Mesozoic]. Holotype, SGO.PI.3119 (n = 1 valve) (Río Tinguiririca, San Fernando, Chile) (Pérez & Reyes, 1989: 11, pl. 2, fig. 10). *Pterotrigonia (?) undulata* (Philippi, 1899), which would require renaming due to the homonymy, but Cooper (2015: 21) stated that Philippi’s species was “based on generically-indeterminate internal moulds and thus *nomina dubia*.”
- unioniformis*, *Trigonia* “?” – Philippi, 1899: 93, pl. 38, figs. 9, 9a. Portezuelo del Tinguiririca, San Fernando, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 27). *Trigonia (?) unioniformis* Philippi, 1899.
- volckmanni*, *Trigonia* – Philippi, 1899: 72, pl. 32, fig. 5, 5a. Junta de Manflas, Copiapó, Chile; Herm. Volckmann; [Mesozoic]. Holotype, SGO.PI.3120 (n = 1 valve) (Junta de Manflas, Copiapó, Chile) (Pérez & Reyes, 1989: 10, pl. 2, figs. 17–18). *Steinmannella (S.) volckmanni* (Philippi, 1899).
- williamsi*, *Trigonia* – Philippi, 1899: 72, pl. 32, fig. 4, 4a. Curi-Ninque, Talca, Chile; Ernesto Williams; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 22–23). *Steinmannella (S.) williamsi* (Philippi, 1899).

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“*clavellata*, *Trigonia*” – Philippi, 1899: 63, pl. 29, figs. 1–4. Philippi identified a specimen from Chile as *Trigonia clavellata* “var.” to indicate that it was possibly a variety of the species described by Parkinson in 1811 from the United Kingdom. However, Philippi did not formally name this variety. Perez & Reyes (1989: 9, pl. 1, fig. 15) found the specimen illustrated by Philippi (SGO.PI.3112), but erroneously designated it as a “lectotype”. In fact, Philippi’s specimen is merely a hypotype (figured specimen) and is not a name-bearing type.

## Unionidae

- ambiguus*, *Unio* – Philippi, 1847z3: 47 [7], pl. 3, fig. 2, ex Parreyss ms. Australia; Parreyss. *Velesunio ambiguus* (Philippi, 1847) (Iredale, 1934: 62–63, pl. 3, fig. 8, pl. 4, fig. 8; McMichael & Hiscock, 1958: 388–395, pl. 1, figs. 1–14, pl. 2, figs. 1–5, pl. 17, figs. 2–3; Haas, 1969: 491–492). Syntypes,



- NHMUK 1841.4.29.103/1 (51.0 mm x 35.9 mm); NHMUK 1841.4.29.103/2 (47.1 mm x 30.8 mm) (as "holotype" and "paratype" in Johnson, 1971: 79). Johnson (1971: 79) stated "While there is no evidence that this specimen [NHMUK 1841.4.29/103/1] was the one figured by Philippi, it is probably as close to an authentic type as can be found." Listed by Sherborn (1923: 252) as by Parreyss, but it is clear that Philippi is its author. Not preoccupied by *Castalia ambigua* Lamarck, 1819, which was occasionally placed in *Unio* but does not belong there. Hence, *Unio philippianus* Küster, 1861, was an unnecessary replacement name (Iredale, 1934: 62; McMichael & Hiscock, 1958: 390). The attempt by Iredale (1934: 63) to restrict the type locality to "King George's Sound" was in error, as Philippi's species is not found in Western Australia.
- aradae*, *Unio* – Philippi, 1844g: 49. Francofonte, Siracusa, Sicily, Italy. Syntype, SMF 316416 (n = 1) (77.7 mm x 35.4 mm). Perhaps a synonym of *Unio mancus* Lamarck, 1819, or of *Unio elongatus gargottae* Philippi, 1836 (Zilch, 1967: 71; Haas, 1969: 39), but more likely of *Unio elongatulus* Megerle von Mühlfeld, in Rossmassler, 1835 (A. Bogan, pers. commun., March 2013).
- araucanus*, *Unio* – Philippi, 1847z3: 50 [10], pl. 4 ["VI"], fig. 3. Southern Chile. Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 178; 1969: 511).
- atrovirens*, *Anodonta* – Philippi, 1849h: 130. Nicaragua; Largilliert. Lectotype, Muséum de Rouen (38 mm x 25 mm), designated by Haas (1930b: 321–322, fig. 2); paralectotype, SMF 5164 (fide Zilch, 1967: 132; not seen in 2013). Synonym of *Anodontites trigonus montezuma* (Lea, 1841) (Haas, 1930b: 321–322). Some authors used *Anodonta inaequivalva* (Lea, 1868) as the name for this species, which is incorrect as Lea's 1868 name does not have priority.
- auratus*, *Unio* – Philippi, 1847z3: 49 [9], pl. 4 ["VI"], fig. 1, ex Lea ms. Insulae Chiloe, Chile. Synonym of *Diplodon chilensis* (Gray, 1828), from Chile (Haas, 1930a: 178; 1969: 511).
- aztecorum*, *Unio* – Philippi, 1847r: 95; 1849f: 15–16 [27–28], pl. 6, fig. 2. Mexico; Liebmman. *Nephronaias aztecorum* (Philippi, 1847) (Haas, 1969: 194–195).
- casaeblancae*, *Unio* – Philippi, 1849i: 176; Pfeiffer, 1869b: 481, pl. 104, figs. 1, 2, as *Unio "casablancae."* Valparaiso & Santiago, Chile; E. B. Philippi. Synonym of the South American *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 178; 1969: 511).
- colchaguensis*, *Unio* – Philippi, 1869b: 47; Pfeiffer, 1869b: 484–485, pl. 104, figs. 9, 10. Near San Fernando, Colchagua, Chile. Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 178; 1969: 512).
- cornea*, *Anodonta* – Philippi, 1849h: 130. Nicaragua; Largilliert. Lectotype, Muséum de Rouen (33.5 mm x 29.2 mm), designated by Haas (1930b: 321, fig. 3); paralectotype, SMF 5163 (fide Zilch, 1967: 132; not seen in 2013); possible paralectotype MNHNS 50893 (n = 1 valve) (27.6 mm x 22.0 mm). Synonym of *Anodontites trigonus montezuma* (Lea, 1841) (Haas, 1930b: 321–322).
- cyamus*, *Unio* – Philippi, 1851c: 125. South Africa; Largilliert. Syntype, Muséum de Rouen (Haas, 1936: 48–49, pl. 4, fig. 1a). Synonym of *Cafferia caffer* Krauss, 1848 (Haas, 1969: 155; Daget, 1998: 69, both as "*caffra*").
- cyrenoides*, *Unio* – Philippi, 1847r: 93–94; 1848i: 79 [11], pl. 5, fig. 1. Lago Nicaragua; Largilliert. Syntype, MNHNS 50199 (n = 1 valve) (42.8 mm x 36.0 mm). *Arotonaias cyrenoides* (Philippi, 1847) (Johnson, 1999: 66; omitted by Haas, 1969); type species (SD Frierson, 1927) of *Arotonaias* Martens, 1900 [Feb.], and (OD) of *Ptychoderma* Simpson, 1900 [8 Oct.].
- diplodon*, *Unio* – Philippi, 1869b: 46; Pfeiffer, 1869b: 483–484, pl. 104, figs. 7, 8. Río Angachilla, Valdivia, Chile. Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 178; 1969: 512).
- foncki*, *Unio* – Philippi, 1869b: 49; Pfeiffer, 1869b: 483, pl. 104, figs. 5, 6. Puerto Montt, Llanquihue, Chile; Fr. Fonck. Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 178–179; 1969: 512). Syntype, SMF 4322 (n = 1) (58.2 mm x 31.3 mm). Haas (1930a: 179) and Zilch (1967: 123) also listed SMF 3852 as a syntype, but it is from Río Guayellua, and may not be original material.
- fulmineus*, *Unio* – Philippi, 1847z3: 46–47 [6–7], pl. 3, figs. 5, 6, ex Parreyss ms. Australia; Parreyss. Synonym of *Parreysia corrugata* (Müller, 1774) (Haas, 1969: 118). Possible syntypes, NHMUK 1841.4.18.135–138 (n = 4) (Johnson, 1971: 84). Sherborn (1926: 2544) listed this as by Parreyss, but it is clear that Philippi is its author.
- gargottae*, *Unio* – Philippi, 1836a: viii, 66, pl. 5, fig. 6, 6a; 1844g: 48. Rivers of northern Sicily, Italy. Synonym of *Unio elongatulus* Megerle von Mühlfeld, in Rossmassler, 1835 (A.



- Bogan, pers. commun., March 2013); Haas (1969: 38–39) as *Unio elongatulus gargottae*. Syntype, SMF 316415 (n = 1) (Sicily) (56.9 mm x 25.2 mm).
- ianthinus*, *Unio* – Philippi, 1869b: 46–47; Pfeiffer, 1869b: 485–486, pl. 104, figs. 11, 12. Santiago, Chile. Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 178 (as “*janthinus*”); 1969: 512).
- incarum*, *Anodonta* – Philippi, 1869a: 40; Pfeiffer, 1869b: 488, pl. 105, figs. 9–11. Río Tambo, Peru. Syntypes, MNHNS 50821 (n = 4 valves) (largest, 144.1 mm x 93.1 mm). Synonym of *Anodontites trigona* (Spix & Wagner, 1827) (Haas, 1969: 561), or a valid species of *Anodontites* (Ramírez et al., 2003: 273).
- jacobaeus*, *Unio* – Philippi, 1869b: 44; Pfeiffer, 1869b: 478, pl. 103, figs. 3, 4. Santiago, Chile. Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 178–179; 1969: 512). Syntype, SMF 3850 (n = 1) (Santiago) (60.3 mm x 33.4 mm) (Haas, 1930a: 179; Zilch, 1967: 123).
- landbecki*, *Unio* – Philippi, 1869b: 45; Pfeiffer, 1869b: 479, pl. 103, figs. 5, 6. Vichuquea, Colchagua, Chile; Landbeck. Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 178; 1969: 512).
- largillierti*, *Unio* – Philippi, 1847r: 94. Yucatan, Mexico; Largilliert. *Potamilus largillierti* (Philippi, 1847). Lectotype MCZ 155569 (70.6 mm x 35.9 mm) (designated by Johnson, 1951a: 77–80, pl. 5, fig. 2); 1 paralectotype MCZ 184531 (65.4 mm x 30.5 mm).
- liebmanni*, *Unio* – Philippi, 1847r: 90; 1849f: 15 [27], pl. 6, fig. 1. Mexico; Liebmann. *Sphenonaias liebmanni* (Philippi, 1847) (Haas, 1969: 205). Type species (OD) of *Sphenonaias* Crosse & P. Fischer, 1894.
- lithophagus*, *Unio* – Philippi, 1847z3: 45 [5], ex Parreyss ms. Published in synonymy of *Unio teretiusculus* Philippi, 1847, from northern Africa. Haas (1936: 81) incorrectly listed “Ziegler” as Philippi’s source of this name.
- longus*, *Unio* – Philippi, 1869b: 44–45; Pfeiffer, 1869b: 477, pl. 103, figs. 1, 2. Río Maulin, Valdivia, Chile. Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 178; 1969: 512).
- mexicanus*, *Unio* – Philippi, 1847r: 95; 1849f: 16 [28], pl. 6, fig. 3. Mexico; Liebmann. *Sphenonaias mexicana* (Philippi, 1847) (Haas, 1969: 206).
- molinae*, *Unio* – Philippi, 1847z3: 50 [10], pl. 4 [“VI”], fig. 4. Southern Chile. Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 179; 1969: 512).
- montanus*, *Unio* – Philippi, 1869b: 48–49; Pfeiffer, 1869b: 482, pl. 104, figs. 3, 4. Mountain rivers, Valdivia, Chile. Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 178; 1969: 512).
- multidentatus*, *Unio* – Philippi, 1847z3: 46 [6], pl. 3, fig. 4, ex Parreyss ms. Australia; Parreyss. Synonym of *Parreysia corrugata* (Müller, 1774) (Prashad, 1936: 120; (Haas, 1969: 118). Listed by Sherborn (1928: 4186) as by Parreyss, but it is clear that Philippi is its author. Type species (M) of *Parreysia* Conrad, 1853.
- nicaraguae*, *Anodonta* – Philippi, 1849h: 130. Nicaragua; Largilliert. Synonym of *Anodontites trapesialis* (Lamarck, 1819) (Haas, 1969: 569). Lectotype, Muséum de Rouen (71.5 mm x 44.5 mm), designated by Haas (1930b: 322–324, fig. 1); paralectotypes, Muséum de Rouen (n = 2, 71 mm x 45 mm; 67 mm x 39 mm); 1 paralectotype, SMF 5106 (as “syn-type” in Zilch, 1967: 131); 1 paralectotype, MCZ 184530 (64.0 mm x 39.9 mm) (erroneously designated as “lectotype” in Johnson, 1951a: 80–82, pl. 5, fig. 1; see Johnson, 1951b); 1 paralectotype MCZ 17071 (62.9 mm x 36.5 mm).
- nuculinus*, *Unio* – Philippi, 1849i: 176. Nicaragua; Largilliert. Synonym of *Micronaias arata* (Lea, 1845) (Haas, 1969: 212). Syntype, ZMB 117922 (n = 1) (17.4 mm x 10.1 mm) (figured, Martens, 1900: pl. 39, fig. 6).
- osbeckii*, *Unio* – Philippi, 1844z: 164; 1847z3: 45–46 [5–6], pl. 3, fig. 1. Yang-tse River. China; Largilliert. Synonym of *Nodularia douglasiae* (Gray, in Griffith & Pidgeon, 1833) (Haas, 1969: 56).
- parreyssi*, *Unio* – Philippi, 1848i: 81 [13], pl. 5, fig. 6, ex Busch ms. Sennar, White Nile; Kotschy. The name was credited to Busch by Sherborn (1929: 4766), but the description was signed by Philippi. Synonym of *Coelatura aegyptiaca* (Cailliaud, 1827) (Haas, 1936: 69; Haas, 1969: 175; Daget, 1998: 25). Pallary (1924: 46, pl. 3, fig. 19) figured the “cotype du Canal Mahmoudieh”, which is actually the specimen figured by Pallary (1909: 78, pl. 5, fig. 6), not a name-bearing type specimen.
- psammactinus*, *Unio* – Philippi, 1848i: 79–80 [11–12], pl. 5, fig. 2, ex Bronn ms. Rio de Janeiro, Brazil. Syntypes, SMF 316750 (n = 4 valves) (largest 48.8 mm x 27.3 mm). This name was credited to Bronn by Sherborn



(1929: 5190), but the description was signed by Philippi. Synonym of *Diplodon granosus* (Bruguière, 1792) (Haas, 1969: 525).

*solidulus*, *Unio* – Philippi, 1869b: 45–46; Pfeiffer, 1869b: 480–481, pl. 103, figs. 9, 10. Santiago, Chile. *Diplodon solidulus* (Philippi, 1869) (Haas, 1930a: 184; Zilch, 1967: 126; Haas, 1969: 516–517; Valdovinos, 1999: 154; Letelier et al., 2003: 120). Type species (OD) of *Australis* Bonetto, Tassara & Rumi, 1987.

*subrostrata*, *Anodonta* – Philippi, 1869a: 39–40. East of Paucartambo, Río Madre de Dios, Peru. Synonym of *Anodontites trigona* (Spix & Wagner, 1827) (Haas, 1969: 560).

*subsinuata*, *Anodonta* – Philippi, 1869a: 41; Pfeiffer, 1869b: 487–488, pl. 105, figs. 7, 8, *non Anodon subsinuatus* G. B. Sowerby II, 1867. Río Ucayali, Peru. Synonym of *Anodontites tenebricosa* (Lea, 1834), and thus unnecessarily renamed *Glabaris philippianus* Simpson, 1900. Haas (1969: 563–564) used *Anodontites carinatus pastasanus* (Clessin, 1879) as the next available name for Philippi's taxon, but Lea's name is a senior synonym.

*subtrapezius*, *Unio* – Philippi, 1847r: 88; 1848i: 80 [12], pl. 5, fig. 3. Locality unknown. Synonym of the South American *Rhipidodonta variabilis* (Maton, 1811).

*teretiusculus*, *Unio* – Philippi, 1847z3: 45–46 [5–6], pl. 3, fig. 3. White Nile; Parreyss. Syntype, MNHNS 50170 (39.3 mm x 15.5 mm). The African *Nitia teretiuscula* (Philippi, 1847) (Haas, 1936: 81–82, pl. 6, fig. 11; Haas, 1969: 158; Daget, 1998: 76–77). Type species (OD) of *Nitia* Pallary, 1924.

*ucayalensis*, *Anodonta* – Philippi, 1869a: 40. Ucayali, Peru. Synonym of *Anodontites trigona* (Spix & Wagner, 1827) (Haas, 1969: 560).

*valdivianus*, *Unio* – Philippi, 1869b: 48; Pfeiffer, 1869b: 479–480, pl. 103, figs. 7, 8. Valdivia, Chile. Syntypes SMF 3849 (8 valves) (largest 48.9 mm x 26.9 mm) (Haas, 1930a: 179; SMF 3851 (2 valves) (Haas, 1930a: 179; Zilch, 1967: 123). Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1930a: 178–179; 1969: 512).

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*“chiloensis, Unio”* – Clessin, 1874 [in Küster & Clessin, 1838–1876]: 161, pl. 35, fig. 6, ex Philippi ms. Chile. Possible syntypes SMF 316738 (n = 2) (largest, 66.1 mm x 38.3 mm). Synonym of *Diplodon chilensis* (Gray, 1828) (Haas, 1969: 512).

*“chinensis, Anodonta”* – Küster, 1842 [in Küster & Clessin, 1838–1876]: 51–52, pl. 12, fig. 3, ex Philippi ms. China. This species was listed by Sherborn (1930: 5979) as a Philippi species, but the description is by Küster alone, with the remarks discussing Philippi in the third person. Küster's species is a synonym of *Cristaria tenuis* (Gray, in Griffith & Pidgeon, 1833) (for the latter: Petit & Coan, 2008: 229).

#### Lucinidae

*antarctica, Lucina* “?” – Philippi, 1855a: 209; 1856: 100; 1865e: 166. Strait of Magellan, Chile. *Nomen dubium* (Holmes et al., 2005: 678–679), or *Lucinoma antarctica* (Philippi, 1855) (Bernard, 1983: 29). This species may be a senior synonym of *Lucinoma lamellata* (E. A. Smith, 1881) (Osorio & Reid, 2004: 82; Güller & Zelaya, 2016a: Supplementary Materials, at 4).

*araucana, Lucina* – Philippi, 1887a: 182 [1887b: 175], pl. 24, fig. 2. Millanejo, Chile; Francisco J. Ovalle; Tertiary.

*brasiliensis, Lucina* – Philippi, 1849h: 150. Rio del Janeiro, Brazil; Kröyer. Syntype, MNHNS 218 (n = 1) (16.3 mm x 15.9 mm). Philippi (1850g: 102 [6], pl. 2, fig. 3) later synonymized his species with *Lucina cryptella* d'Orbigny, 1846. Huber (2015: 421) was evidently under a misapprehension that d'Orbigny's figures for this species (pl. 84, figs. 18–20), miscaptioned as *Lucina brasiliensis*, appeared in 1842, but this plate was not published until 1846. Thus, the species should be known as *Loripes cryptella* (d'Orbigny, 1846).

*bullata, Lucina* – Philippi, 1847r: 76; 1850g: 101 [5], pl. 2, fig. 1. Locality unknown. Perhaps an earlier name for the southwestern Pacific-Australian *Anodontia* (*Cavatidens*) *bullula* (Reeve, 1850), but probably best regarded as a *nomen dubium*; type material not located (Taylor & Glover, 2005: 323–325, figs. 11B, 12B, 34, 41G–L; Huber, 2015: 456).

*cancellaris, Lucina* – Philippi, 1846h: 21. Mazatlán, Sinaloa, Mexico. SBMNH 149738, neotype from Cabo Haro, Sonora, Mexico. The Panamic *Radiolucina cancellaris* (Philippi, 1846) (Coan & Valentich-Scott, 2012: 358–360, pl. 116 (neotype); Garfinkle, 2012: 23–25; Huber, 2015: 419).

*chemnitzii, Lucina* – Philippi, 1849i: 151. Yucatan; Largilliert. Synonym of *Divaricella dentata* (W. Wood, 1815) (J. Taylor, pers. commun., July 2013).



- chrysostoma*, *Lucina* – Philippi, 1845x: 181; 1847j: 206 [2], pl. 1, fig. 3. Locality not stated. Synonym of the western Atlantic *Anodontia* (*Anodontia*) *alba* Link, 1807 (Taylor & Glover, 2005: 292–297, figs. 11A, 12A, 13, 14).
- clausa*, *Lucina* – Philippi, 1849i: 151; 1850g: 101–102 [5–6], pl. 2, fig. 2. Locality unknown. Syntype, MNHNS 191 (figured specimen; labeled as from “Seychelles”) (n = 1) (29.1 mm x 28.2 mm). *Loripes clausus* (Philippi, 1849), which occurs from the Red Sea to Mozambique (Oliver, 1992: 97, pl. 20, fig. 2a, b, as “1848”; Huber, 2015: 75, 420–421).
- commutata*, *Lucina* – Philippi, 1836a: viii, 32, pl. 3, fig. 15a–c; 1844g: 25, 26. Sicilian Sea; also fossil. Possible syntypes, SMF 315904 (n = 3) (largest, 7.6 mm x 6.6 mm). Synonym of *Lucinella divaricata* (Linnaeus, 1758) (Sabelli et al., 1990: 300; Kantor & Sysoev, 2005: 347); type species (OD) of *Lucinella Monterosato*, 1883.
- cycloides*, *Trigonia* – Philippi, 1899: 87, pl. 37, figs. 1, 2, 2a. Río Tinguiririca, San Fernando, Chile; Frid. Albert; [Mesozoic]. Lectotype, SGO.PI.3143 (n = 1 valve), designated by Pérez & Reyes (1989: 20, pl. 4, fig. 10); paralectotype, SGO.PI.3144 (n = 1). Pérez & Reyes (1989) determined that this species was referable to the Lucinidae, genus unknown, but comparable to *Lucina leufuensis* Weaver, 1931, from Argentina.
- divergens*, *Lucina* – Philippi, 1850g: 103 [7], pl. 2, fig. 4. Pacific Ocean “?”; E. B. Philippi. The Red Sea and Indian Ocean *Ctena divergens* (Philippi, 1850) (Mienis, 1994; Zuschin & Oliver, 2003: 105, pl. 22, figs. 6–10; Huber, 2015: 88, 438).
- foncki*, *Trigonia* – Philippi, 1899: 89–90, pl. 38, fig. 1, 1a. Valle de Yeso, Santiago, Chile, 8,500'; Guil. Münnich; [Mesozoic]. Holotype, SGO.PI.3148 (Pérez & Reyes, 1989: 20, pl. 3, figs. 15–17). Pérez & Reyes (1989) determined that this species was referable to the Lucinidae, genus unknown.
- fragilis*, *Lucina* – Philippi, 1836a: viii, 34; 1844g: 25–26; Philippi, 1845x: 181. Palermo, Sicily, Italy; also fossil (Palermo and Militello, Sicily). Syntype, ZMB 2038 (n = 1 valve) (Palermo) (10.3 mm x 9.0 mm). *Loripinus fragilis* (Philippi, 1836) (Sabelli et al., 1990: 301; Taylor & Glover, 2005: 325, figs. 11B, 12B, 42A, 42B; Taylor et al., 2011: 31; Huber, 2015: 104, 457). Type species (SD Martens, 1884) of *Loripinus Monterosato*, 1883.
- glabrata*, *Trigonia* – Philippi, 1899: 87–88, pl. 37, fig. 3, 3a. Río Tinguiririca, San Fernando, Chile; Frid. Albert; [Mesozoic]. Holotype, SGO.PI.3145 (n = 1 valve) (Pérez & Reyes, 1989: 20, pl. 3, fig. 13). Pérez & Reyes (1989) determined that this species was referable to the Lucinidae, genus unknown.
- lebuensis*, *Lucina* “?” – Philippi, 1887a: 182 [1887b: 175], pl. 24, fig. 3. Lebu; Tertiary. Holotype, SGO.PI.343 (n = 1 valve).
- lupinus*, *Lucina* – Philippi, 1887a: 182–183 [1887b: 176], pl. 24, fig. 8. Lebu, Chile; Tertiary. Holotype, SGO.PI.346 (n = 1).
- mactroides*, *Trigonia* – Philippi, 1899: 84, pl. 36, fig. 2, 2a, 2b. Río Tinguiririca, San Fernando, Chile; Moses Amaral; [Mesozoic]. Holotype, SGO.PI.3137 (Pérez & Reyes, 1989: 19, pl. 5, figs. 1, 2, 5). Pérez & Reyes (1989) determined that this species was referable to the Lucinidae, genus unknown.
- muennichi*, *Trigonia* – Philippi, 1899: 73, pl. 33, fig. 2, 2a, as “*T. münnichi*”. Valle del Yeso, Santiago, Chile; Tr. Fonck; Guill. Münnich; [Mesozoic]. Holotype, SGO.PI.3121 (Pérez & Reyes, 1989: 19, pl. 4, figs. 7, 11). Pérez & Reyes (1989) determined that this species was referable to the Lucinidae, genus unknown.
- navidadis*, *Lucina* – Philippi, 1887a: 182 [1887b: 175–176], pl. 24, fig. 5. Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.339 (n = 1 valve); SGO.PI.4792 (n = 1 valve).
- obliqua*, *Lucina* – Philippi, 1850g: 105 [9], pl. 2, fig. 8, *non* DeFrance, 1823, *non* Goldfuss, 1840. West America “Ora America occidentalis?”. Presumed *nomen dubium* (Huber, 2015: 440).
- patagonica*, *Fimbria* “?” – Philippi, 1887a: 183 [1887b: 177], pl. 24, fig. 11. Santa Cruz, Chile; Ramón Vidal Gormáz; Tertiary. Syntype, SGO.PI.427 (n = 1 valve, labeled as “lectotipo”); SGO.PI.4793, 4794 (n = 1 valve each; both labeled as “paralectotipo”). Parodiz (1996: 225) stated that this species “is of questionable taxonomic position.”
- pisum*, *Lucina* – Philippi, 1850g: 105 [9], pl. 2, fig. 9, *non* J. De C. Sowerby, in Fitton, 1836. Mazatlán, Sinaloa, Mexico. *Divaricella parvula* Dall, 1901, *nom. nov. pro* *L. pisum* Philippi, *non* J. De C. Sowerby, in Fitton. *Lucina pisum* Reeve, 1850 (Australia, now *Cardiolucina eucosmia* (Dall, 1901)) is a junior homonym as Philippi’s name was described in March 1850, Reeve’s in August 1850. The Panamic *Divalinga perparvula* (Dall, 1901) (Bernard, 1983: 29; Coan & Valentich-Scott, 2012: 343, 345, pl. 111).



*plicata*, *Lucina* – Philippi, 1887a: 183 [1887b: 176], pl. 24, fig. 9. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.626 (n = 1 valve).

*promaucana*, *Lucina* – Philippi, 1887a: 181–182 [1887b: 175], pl. 24, fig. 6. Navidad, Matanzas, Lebu & Santa Cruz, Chile; Tertiary. Syntypes, SGO.PI.340 (n = 2, from Lebu); SGO.PI.342 (n = 1, from Matanzas); SGO.PI.344 (n = 12, from Santa Cruz); SGO.PI.345 (n = 6 valves, from Navidad); SGO.PI.4786–4789 (n = 1 valve each, all from Matanzas, labeled as “paralectotipo”). *Lucina promaucana* Philippi, 1887, Miocene (Tavera, 1979: 84, pl. 14, figs. 27–28); *Lucinoma promaucana* (Philippi, 1887); Miocene (Frassinetti & Covacevich, 1994: 83, figs. 15–17; Frassinetti, 2004: 74).

*similis*, *Lucina* – Philippi, 1887a: 182 [1887b: 176], pl. 24, fig. 7. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.347 (n = 1 valve).

*sowerbyana*, *Lucina* – Philippi, 1887a: 180–181 [1887b: 174], pl. 37, fig. 10, after G. B. Sowerby I, 1846. Puerto de Hambre, Chile; Cretaceous. Philippi stated that this was for “*Lucina excentrica* Sow., Darw., Geol. Obs., Taf. V, Fig. 21, ohne Beschreibung [without description].” However, G. B. Sowerby I, in Darwin (1846: 267) provided both an illustration and a full description of this species, so that Philippi’s name was an unnecessary renaming.

*subpentagona*, *Lucina* “?” – Philippi, 1887a: 181 [1887b: 174], pl. 23, fig. 9. Algarrobo, Chile; Cretaceous.

*tenuis*, *Lucina* – Philippi, 1887a: 182 [1887b: 175], pl. 24, fig. 4, *non* J. Müller, 1851, *non* Deshayes, 1857. Lomas Tucapel, near Lebu, Chile; Tertiary. Syntypes, SGO.PI.341 (n = 1 valve), SGO.PI.4790, 4791 (n = 1 valve each, labeled as “paralectotipo”).

*textilis*, *Lucina* – Philippi, 1850g: 104–105 [8–9], pl. 2, fig. 7. Locality unknown. Synonym of the western Atlantic *Clathrolucina costata* (d’Orbigny, 1846) (Taylor et al., 2013).

*veneriformis*, *Trigonia* – Philippi, 1899: 89, pl. 37, fig. 6, 6a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Holotype, SGO.PI.3147 (Pérez & Reyes, 1989: 20, pl. 5, fig. 4). Pérez & Reyes (1989) determined that this species was referrable to the Lucinidae, genus unknown.

*venusta*, *Lucina* – Philippi, 1847j: 206 [2], pl. 1, fig. 2. Locality unknown. The southeast Asian *Lepidolucina venusta* (Philippi, 1847); type species (OD) of *Lepidolucina* Glover &

Taylor, 2007 (Glover & Taylor, 2007: 142–144, fig. 21A, B, E–H; Huber, 2015: 72, 419).

*vidali*, *Artemis* – Philippi, 1887a: 113 [1887b: 107–108], pl. 15, fig. 2. Navidad & Matanzas, Chile; Tertiary. Syntypes, SGO.PI.458 (n = 4 valves, Matanzas); SGO.PI.704 (n = 1, Navidad); SGO.PI.705 (n = 1, Navidad). Frassinetti (1975: 222–223, figs. 5–6; 1978: 52–53, pls. 1–2) referred to SGO.PI.704 as the “holotipo” and SGO.PI.705 as the “para-tipo,” but neither was designated as such by Philippi. Type species (OD) of *Matanziella* Frassinetti, 1978. *Miltha* (*Matanziella*) *vidali* (Philippi, 1887); Miocene (Frassinetti & Covacevich, 1994: 84, figs. 18, 19; DeVries & Frassinetti, 2003: 124, pl. 1, fig. 7).

### Thyasiridae

*Ptychina* – Philippi, 1836a: vii, 15; 1845i: 75; 1845j: 91. Type species (M): *Ptychina biplicata* Philippi, 1836a. Synonym of *Thyasira* Lamarck, 1818, ex Leach ms. (Chavan, 1969a: N508).

*biplicata*, *Ptychina* – Philippi, 1836a: vii, 15, pl. 2, fig. 4a–c; 1844g: 11–12; 1844z3: [1]; 1845j: 91, as *Axinus biplicatus*. Mediterranean, in “deep water”; Neapolitan Sea. Also fossil at Palermo, Sicily, Italy. Possible syntypes, PHB MB M.545 (M) 33 (n = 3) (missing in 2013). Formerly listed as a synonym of *Thyasira flexuosa* (Lamarck, 1818) (Sabelli et al., 1990: 301), it is now considered a distinct, larger Mediterranean species (Giribet & Peñas, 1997: 57 [19], 86 [48], fig. 98; Repetto et al., 2005: 308, fig. 1422; Huber, 2015: 61).

*chilensis*, *Thyasira* – Philippi, 1887a: 184 [1887b: 177], pl. 23, fig. 8. Navidad, Chile; Tertiary [Miocene]. SGO.PI.630, holotype. Also probably Pliocene (Frassinetti, 1997: 65, 68–69, pl. 1, figs. 15, 16).

*gouldii*, *Lucina* – Philippi, 1845g: 75. Massachusetts. For *Lucina flexuosa sensu* Gould (1841: 72), *non* Montagu, 1803. The type material would be Gould’s specimens from Massachusetts Bay (U.S.A.) (which were not found at the MCZ in 2013); the “syntypes” cataloged as NHMUK 1843.6.30.304–306 (“Greenland”) are thus not type specimens. The North Atlantic *Thyasira gouldii* (Philippi, 1845) (Killeen & Oliver, 2002; Oliver & Killeen, 2002: 30–34, figs. 2C, 6B, 10A, 11–13; Kantor & Sysoev, 2005: 347; Huber, 2015: 387, all as *T. “gouldi”*), which is now treated as a distinct species from *T. flexuosa* (Montagu, 1803).



*nystii*, *Axinus* – Philippi, 1845h: 91, *nom. nov. pro Axinus angulatus* “de Koninck”, 1838 [actually Nyst, 1835], *non* J. Sowerby, 1821. Belgium; fossil. The Oligocene *Thyasira nystii* (Philippi, 1845) (Glibert & Van de Poel, 1967: 14, as “*T. nysti*”). However, now considered a synonym of *Thyasira benedeni* (de Koninck, 1838) (Marquet, 2010: 264–265, pl. 2, fig. 1, pl. 3, fig. 8).

*sarsii*, *Axinus* – Philippi, 1845h: 91. Norway. The North Atlantic *Thyasira sarsii* (Philippi, 1845) (Oliver & Killeen, 2002: 36–38, figs. 2D, 6D, 14; Kantor & Sysoev, 2005: 347; Oliver, 2014, 122–124, all as *T. “sarsi”*; Huber, 2015: 63, 396, as “*sarsi*”).

*sinuatus*, *Axinus* – Philippi, 1845h: 91. Mediterranean & fossil at Palermo, Sicily, Italy. If this is a *Thyasira*, it would be a junior homonym of *Thyasira sinuata* (Lamarck, 1818), described as a *Lucina*, now regarded as a *Thyasira*.

#### Cardiniidae

*atacamensis*, *Cardinia* – Philippi, 1899: 96, pl. 42, fig. 5. Valle de Ternera, Copiapó, Chile; Rémond de Corbineau; [Mesozoic].

*copiapina*, *Cardinia* – Philippi, 1899: 96, pl. 42, fig. 4. Manflas, Copiapó, Chile; [Mesozoic]. Syntype, SGO.PI.5021 (n = 1).

*domeykoi*, *Cardinia* – Philippi, 1899: 95–96, pl. 42, fig. 3. Locality unknown, Chile; Domeyko; [Mesozoic]. Syntypes, SGO.PI.5022 (n = 1, figured specimen); SGO.PI.5023 (n = 1 valve).

*remondi*, *Cardinia* – Philippi, 1899: 95, pl. 25, fig. 6. Valle de la Ternera, Chile; Rémond de Corbineau; [Mesozoic].

#### Carditidae

*analís*, *Cardita* – Philippi, 1845z: 448 [*nomen nudum*]; 1847-l: 50, pl. 7, fig. 6a–c. Osterweddingen & Welsleben, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene; Sack’s collection. *Cyclocardia analís* (Philippi, 1847) (Glibert & Van de Poel, 1970: 110, as “1846”).

*avellana*, *Cardita* – Philippi, 1847-l: 58, pl. 10a, fig. 14a–c. Magdeburg area, Germany; Tertiary; Hayseschen collection. Koenen (1893: 1241) suggested that Philippi’s species might be a juvenile of *Cardita suborbicularis* Sandberger, 1863.

*corbis*, *Cardita* – Philippi, 1836a: viii, 55, pl. 4, fig. 19; 1844g: 41. Palermo, Sicily, Italy.

Also fossil, Nizzeti, Sicily. Syntypes, PHB MB M.\_\_\_\_ (V) 60 (circa 15 valves) (Nizzeti, near Catania). The eastern Atlantic *Coripia corbis* (Philippi, 1836) (Cretella et al., 2005: 127, as *Pteromeris (Coripia)*; Huber, 2010: 257, 659). Mienis (2000) explained that some Italian authors had erroneously listed *Pteromeris minuta* (Scacchi, 1836) as a senior synonym of Philippi’s species. Fischer (1887: 1187) and Chavan (1969b: N554) incorrectly stated that this was the type species of *Coripia* De Gregorio, 1885; however, De Gregorio listed Philippi’s name in the synonymy of *Cardita unidentata* (Basterot, 1825) (originally described in *Venericardia*), which is the type species of *Coripia*, by monotypy (Pras, 2013: 15–16).

*dunkeri*, *Cardita* – Philippi, 1847-l: 50, pl. 7, fig. 7a–c. Magdeburg area, Germany; Tertiary; Sack’s collection & Altenweddigen. Figured syntype, PHB MB M.6317 (V) 56 (1 valve) (labeled as “holotype” but actually a syntype) (24.7 mm x 26.0 mm). *Cardita dunkeri* Philippi, 1847 (Koenen, 1893: 1237–1239, pl. 84, figs. 7–10).

*elongata*, *Cardita* – Philippi, 1845i: 54–55. “Pacific Ocean”.

*excisa*, *Cardita* – Philippi, 1847r: 91–92. Hawaii. *Cardita excisa* Philippi, 1847 (Huber, 2010: 654; Severns, 2011: 472–473, pl. 216, figs. 5, 6).

*inaequalis*, *Cardita* – Philippi, 1887a: 173 [1887b: 167], pl. 37, fig. 5. Santa Cruz, Chile; Ramón Vidal Gormáz; Tertiary. Syntypes, SGO.PI.469 (n = 1 valve, labeled as “lectotipo”); SGO.PI.4752–4758 (labeled as “paralectotipo”). *Cardiocardia inaequalis* (Philippi, 1887), Oligocene-Miocene (Frassinetti & Covacevich, 1999: 26, pl. 5, figs. 1–3); or a synonym of *Fasciculicardia patagonica* (G. B. Sowerby I, 1846) (Griffin & Nielsen, 2008: 277, pl. 13, figs. 6, 7).

*macsporrani*, *Cardita* – Philippi, 1887a: 173 [1887b: 166–167], pl. 28, fig. 2. Lebu, Chile; MacSporran; Tertiary. Holotype, SGO.PI.623 (n = 1).

*magellanica*, *Cardita* – Philippi, 1898b: 89. Seno Almirantazgo, Strait of Magellan, Chile; C. E. Porter, 1895. Synonym of the South American *Cyclocardia velutina* (Smith, 1881); type material not located (Huber, 2010: 656; Güller & Zelaya, 2013: 209–211, figs. 4A–O, 9C, Appendix 4).

*oxytropis*, *Cardita* “?” – Philippi, 1887a: 174 [1887b: 167], pl. 25, fig. 8. Mouth of Río Rapel, Chile; Tertiary.



*promaucana*, *Cardita* – Philippi, 1887a: 174 [1887b: 167], pl. 37, fig. 3. Navidad, Chile; Tertiary [Miocene].

*teretiuscula*, *Cardita* – Philippi, 1849h: 141–142. Locality unknown; Largilliert.

*volckmanni*, *Cardita* – Philippi, 1887a: 173 [1887b: 167], pl. 37, fig. 4, 4a. Tubul, Chile; Volckmann; Tertiary. The Pliocene *Cardiocardita volckmanni* (Philippi, 1887) (Frassinetti & Covacevich, 1995: 53–54, pl. 1, figs. 10–17; Frassinetti, 1997: 65–66, 68–69, pl. 1, figs. 17–20), or a junior synonym of *Cyclocardia velutinus* (E.A. Smith, 1881), Pliocene to Recent (Nielsen & Valdovinos, 2008: 206, fig. 8).

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*“aculeata*, *Cardita*” – Philippi, 1836a: viii, 54, pl. 4, fig. 18. As “mihi” for a transfer of *Chama aculeata* Poli, 1795, to *Cardita*. (Poli’s species was *non* Ström, 1768.) Philippi’s material (non-types), SMF 315658 (4 valves).

#### Condylocardiidae

*australis*, *Cardita* – Philippi, 1858b: 23–24, *non* Lamarck, 1819. Islas Chonos, Chile; Fr. Fonk. Renamed *Actinobolus philippi* Tryon, 1872, who misattributed the species to the Philippine Islands. Synonym of the South American *Carditella naviformis* (Reeve, 1843); type material not located (Bernard, 1983: 34; Güller & Zelaya, 2013: 214–216, figs. 6A–M, 9D, Appendix 6), or a *nomen dubium* (Huber, 2015: 384).

*pygmaeum*, *Cardium* – Philippi, 1860a: 176 [1860b: 158], Zool. pl. 7, fig. 3, *non* Donovan, 1799. Isla Blanca, [Atacama], Chile. Synonym of *Carditella semen* (Reeve, 1843); type material not located (Bernard, 1983: 34; Güller & Zelaya, 2013: 216–218, figs. 7A–O, Appendix 7), or a *nomen dubium* (Huber, 2015: 384).

#### Crassatellidae

*medinae*, *Venus* – Philippi, 1887a: 121 [1887b: 115], pl. 17, fig. 1. Lebu, Chile; Tertiary. Holotype, SGO.PI.115 (n = 1). *Crassatella medinae* (Philippi, 1887) (Frassinetti, 1974: 49, fig. 11).

*minuta*, *Crassatella* – Philippi, 1844z4: 45, [86], pl. 2, fig. 4. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. *Crassatina* (*Chattonia*) *astarteiformis minuta* (Philippi, 1844) (Janssen, 1979b: 99, pl. 3, fig. 51).

*pfeifferi*, *Astarte* – Philippi, 1849h: 133. Cuba; Pfeiffer. Synonym of the western Atlantic *Crassinella lunulata* (Conrad, 1834).

*ponderosa*, *Crassatella* – Philippi, 1887a: 172–173 [1887b: 166], pl. 38, fig. 5, 5a. Lebu and Navidad, Chile; Tertiary. Lectotype, SGO.PI.468 (n = 1 valve, from Navidad), designated by DeVries (2016: 672–674, figs. 8A–C); paralectotypes SGO.PI.4750, 4751 (n = 1 valve, each from Navidad). SGO.PI.4749, although labeled as “paralectotipo” has a note by D. Frassinetti, “No, es *Cucullaea chilensis*”. *Crassatella ponderosa* Philippi, 1887, Miocene (Tavera, 1979: 83–84, pl. 15, fig. 35); *Eucrassatella ponderosa* (Philippi, 1887) (DeVries & Frassinetti, 2003: 124, pl. 2, fig. 3); redescribed by DeVries (2016). Type species (OD) of *Tilicrassatella* DeVries, 2016.

*subquadrata*, *Astarte* – Philippi, 1847-l: 47, pl. 8, fig. 4. Magdeburg area, Germany; Tertiary; Sack’s collection. Philippi, in the “Nachtrag zu den Bivalven” section (1847-l: 57–58) stated that after examining additional material, he realized that this species was not an *Astarte*, but was instead referable to “*Crassatella tenuistriata* Desh. var. A Nyst.” Koenen (1866: 290) later concluded that Philippi’s species was not conspecific with the “var. A” of Nyst, so he renamed it *Crassatella bosqueti* Koenen, 1866, for which he later provided a more complete description (Koenen, 1893: 1204–1207, pl. 82, figs. 5–7). However, Koenen’s taxon was unnecessary, because he simply should have used *Crassatella subquadrata* (Philippi, 1847) for this Oligocene species from northern Germany. Philippi’s species is also a senior homonym of *Crassatella subquadrata* G. B. Sowerby II, 1870 (South Africa), for which a junior synonym, *Crassatella tenuis* G. B. Sowerby III, 1907, is the next available name (D. Herbert, in litt., 1 Oct. 2014).

#### Astartidae

*alberti*, *Trigonia* – Philippi, 1899: 92, pl. 38, fig. 6, 6a. Portezuelo del Tinguiririca, San Fernando, Chile; [Mesozoic]. Holotype, SGO.PI.3152 (n = 1 valve) (Pérez & Reyes, 1989: 18–19, pl. 3, fig. 9). *Astarte* (?) *inconspicua* (Philippi, 1899); Pérez & Reyes (1989) doubtfully transferred this species to the Astartidae.

*anus*, *Astarte* – Philippi, in Volger, 1845: 33, 35; 1847-l: 47–48, pl. 8, fig. 1. Lüneburg,



- Lower Saxony, Germany, [Middle] Miocene. *Carinastarte anus* (Philippi, in Volger, 1845) (R. Janssen, pers. comm., April 2013). Type material lost (R. Janssen, pers. comm., April 2013).
- bipartita*, *Lucina* “?” – Philippi, 1836a: viii, 32–33, pl. 3, fig. 21a–c; 1844g: 25; 1844n: 100–101, as *Astarte bipartita*; 1844z3: 1; 1845u: 60 [6], pl. 1, fig. 9, as *Astarte bipartita*; non DeFrance, 1823. Palermo, Sicily, Italy. Synonym of *Gonilia calliglypta* (Dall, 1903) (Sabelli et al., 1990: 308); Philippi’s taxon is the type species (OD) of *Gonilia* Stoliczka, 1871.
- decipiens*, *Trigonia* – Philippi, 1899: 90, pl. 38, fig. 2, 2a. Portezuelo del Tinguiririca, San Fernando, Chile; [Mesozoic]. Holotype, SGO.PI.3149 (n = 1 valve) (Pérez & Reyes, 1989: 18, pl. 3, fig. 11). *Astarte* (?) *inconspicua* (Philippi, 1899); Pérez & Reyes (1989) doubtfully transferred this species to the Astartidae.
- dilatata*, *Astarte* – Philippi, 1845z: 448 [*nomen nudum*]; 1847-l: 47, pl. 8, fig. 2. Magdeburg area, Germany; Tertiary; Sack’s collection. The Oligocene *Astarte dilatata* Philippi, 1847 (Koenen, 1868: 252–253, pl. 29, figs. 5a–5k; Glibert & Van de Poel, 1970: 74, as “1846”; R. Janssen, pers. comm., April 2013).
- fallax*, *Trigonia* – Philippi, 1899: 90–91, pl. 38, fig. 3. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Lectotype, SGO.PI.3123 (n = 1 valve), designated by Pérez & Reyes (1989: 18, pl. 3, fig. 12). Synonym of *Astarte* (?) *inconspicua* (Philippi, 1899); Pérez & Reyes (1989) doubtfully transferred this species to the Astartidae.
- gregaria*, *Astarte* – Philippi, 1860a: 143 [1860b: 126], Petref. pl. 4, fig. 4. Desierto de Atacama, Chile; [Mesozoic or Cenozoic?].
- humilis*, *Trigonia* – Philippi, 1899: 88, pl. 37, fig. 4. Portezuelo del Tinguiririca, San Fernando, Chile; [Mesozoic]. Type material not found (Pérez & Reyes, 1989: 28). *Astarte* (?) *humilis* (Philippi, 1899); Pérez & Reyes (1989) doubtfully transferred this species to the Astartidae.
- inconspicua*, *Trigonia* – Philippi, 1899: 89, pl. 37, fig. 7, 7a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Holotype, SGO.PI.3123 (n = 1 valve) (Pérez & Reyes, 1989: 18, pl. 4, fig. 1). *Astarte* (?) *inconspicua* (Philippi, 1899); Pérez & Reyes (1989) doubtfully transferred this species to the Astartidae.
- krugi*, *Trigonia* – Philippi, 1899: 92–93, pl. 38, figs. 8, 8a. Río Tinguiririca, San Fernando, Chile; [Mesozoic]. Holotype, SGO.PI.3153 (n = 1 valve) (Pérez & Reyes, 1989: 19, pl. 5, fig. 6). Synonym of *Astarte* (?) *inconspicua* (Philippi, 1899); Pérez & Reyes (1989) doubtfully transferred this species to the Astartidae.
- trita*, *Trigonia* – Philippi, 1899: 93–94, pl. 38, fig. 10, 10a. Locality unknown, Chile; [Mesozoic]. Holotype, SGO.PI.3154 (Pérez & Reyes, 1989: 19, pl. 4, fig. 2). *Astarte* (?) *trita* (Philippi, 1899); Pérez & Reyes (1989) doubtfully transferred this species to the Astartidae.
- vetula*, *Astarte* – Philippi, in Volger, 1845: 33, 35–36; 1847-l: 48, pl. 8, fig. 3. Lüneburg, Lower Saxony, Germany, [Middle] Miocene. *Carinastarte vetula* (Philippi, in Volger, 1845) (R. Janssen, pers. comm., April 2013). Type material lost (R. Janssen, pers. comm., April 2013).

## Cardiidae

- bellum*, *Cardium* – Philippi, 1897: 368, pl. 5, non Stoliczka, 1871. Punta Pabellon, Isla Chiloé, Chile; [Cenozoic?].
- bolivianum*, *Cardium* – Philippi, 1887a: 179 [1887b: 172–173], pl. 58, fig. 6. Mejillones, Chile; Quaternary.
- bonariense*, *Cardium* – Philippi, 1893b: 11, pl. 1, fig. 10. Argentina; Tertiary. *Trachycardium bonariensis* (Philippi, 1893), Miocene (del Río & Martínez, 1998: 68, pl. 19, fig. 3).
- bravardi*, *Cardium* – Philippi, 1893b: 10, pl. 1, fig. 11. Argentina; Tertiary [Miocene]. Synonym of *Dinocardium platense* (d’Orbigny, 1842) (Griffin & Nielsen, 2008: 281, pl. 14, fig. 8).
- diazii*, *Cardium* – Philippi, 1887a: 175 [1887b: 168–169], pl. 39, fig. 12. Hualpen, Chile; Wenceslao Diaz; Cretaceous. Syntypes, SGO.PI.622 (n = 1, labeled as “lectotipo”); SGO.PI.302 (n = 1 valve; SGO.PI.648 (n = 1 valve); SGO.PI.4759–4769 (all labeled as “paralectotipo”). Synonym of *Cardium* (*Rugicardium*) *acuticostatum* d’Orbigny, 1841 (Wilckens, 1904: 231–237, pl. 19, figs. 7–10), or of *C. (Bucardium) acuticostatum* d’Orbigny, 1841, Maastrichtian (Stinnesbeck, 1986: 174–175, pl. 3, figs. 1–5).
- diminutum*, *Cardium* – Philippi, 1887a: 177 [1887b: 170], pl. 58, fig. 9. Hualpen, Chile; Cretaceous. Syntypes, SGO.PI.301 (n = 1 valve, labeled as “lectotipo”); SGO.PI.4781 (n = 1 valve, labeled as “paralectotipo”). Synonym of *Cardium* (*Rugicardium*) *acuti-*



- costatum* d'Orbigny, 1842 (Wilckens, 1904: 231–237, pl. 19, figs. 7–10).
- distortum*, *Cardium* – Philippi, 1845i: 55. *Insulae Amicorum* [Tonga]. Syntype, SMF 315838 (2 valves) (10.8 mm x 9.1 mm). Status unresolved (Hylleberg, 2004: 473).
- domeykoanum*, *Cardium* – Philippi, 1887a: 178 [1887b: 171], pl. 39, fig. 3, 3a. Coquimbo, Chile; Tertiary [Pliocene]. Holotype, SGO.PI.390 (n = 1). *Trachycardium procerum domeykoanum* (Philippi, 1887) (DeVries & Frassinetti, 2003: 125, pl. 1, fig. 5).
- grande*, *Cardium* – Philippi, 1887a: 177 [1887b: 171], pl. 39, fig. 6. Guayacán, Chile; Tertiary. Syntype, SGO.PI.437 (n = 2 valves, labeled as “paralectotipo”). *Laevicardium (Mexicardia) procerum grande* (Philippi, 1887), Pliocene (Herm, 1969: 116–117, pl. 8, figs. 3–4).
- hausmanni*, *Cardium* – Philippi, 1845z: 448 [nomen nudum]; 1847-l: 49, pl. 7, fig. 5a, b. Magdeburg area, Germany; Tertiary; Sack's collection. The Oligocene *Cardium (Vepricardium) hausmanni* Philippi, 1847 (Glibert & Van de Poel, 1970: 51, as “1846”); *Freneixicardia hausmanni* (Philippi, 1847) (Schneider, 2002: 367–368, fig. 29, as “1846”; Hylleberg, 2004: 545).
- hualpense*, *Cardium* – Philippi, 1887a: 176 [1887b: 169], pl. 39, fig. 5. Hualpen, Chile; Wenceslao Diaz; Algarrobo, Landbeck. Cretaceous. Syntypes, SGO.PI.386 (Hualpen) (n = 1, labeled as “holotipo”); SGO.PI.288 (n = 1, Algarrobo). Synonym of *Cardium (Rugicardium) acuticostatum* d'Orbigny, 1842 (Wilckens, 1904: 231–237, pl. 19, figs. 7–10), or as *C. (Bucardium) acuticostatum* d'Orbigny, 1842, Maastrichtian (Stinnesbeck, 1986: 174–175, pl. 3, figs. 1–5).
- landbecki*, *Cardium* – Philippi, 1887a: 176 [1887b: 170], pl. 57, fig. 3a, 3b. Algarrobo & San Vicente, Chile; Cretaceous. Syntypes, SGO.PI.646 (n = 1, from Algarrobo, labeled as “holotipo”); SGO.PI.287 (n = 2, from San Vicente). Synonym of *Cardium (Bucardium) acuticostatum* d'Orbigny, 1842; Maastrichtian (Stinnesbeck, 1986: 174–175, pl. 3, figs. 1–5).
- magellanicum*, *Cardium* – Philippi, 1887a: 177 [1887b: 170–171], pl. 38, fig. 4. Punta Arenas, Chile; Jorje Schythe; Tertiary. Holotype, SGO.PI.392 (n = 1 valve).
- minimum*, *Cardium* – Philippi, 1836a: viii, 51; 1844g: 38, 40, 299, pl. 14, fig. 18a, 18b. Sicily, Italy. Also fossil. *Parvicardium minimum* (Philippi, 1836) (Sabelli et al., 1990: 310; Giribet & Peñas, 1997: 58 [20]; Aartsen & Goud, 2000: 183; 2001: 121, figs. 4–6, 9, 10, 12; Hylleberg, 2004: 628, but wrongly indicated by Hylleberg as the type species of *Parvicardium*; Janssen & Krylova, 2014: 63), or *Papillacardium minimum* (Philippi, 1836) (Huber, 2010: 302; 2015: 563–564).
- minuta*, *Trigonia* – Philippi, 1899: 68, pl. 30, fig. 8. Valle de Tinguiririca, Chile; [Mesozoic]. Holotype, SGO.PI.3117 (Río Tinguiririca, San Fernando, Chile) (Pérez & Reyes, 1989: 16, pl. 3, fig. 8). *Protocardia minuta* (Philippi, 1899). Transferred to the Cardiidae by Pérez & Reyes (1989).
- modestum*, *Cardium* – Philippi, 1849h: 142. China; Largilliert. Type material not found in Muséum de Rouen (Huber, 2015: Chapter 5 on CD). Status unresolved (Hylleberg, 2004: 631).
- multisulcatum*, *Cardium* – Philippi, 1887a: 178 [1887b: 172], pl. 39, fig. 8, *non* Borson, 1825, *non* Hisinger, 1841. No locality, Chile; Francisco J. Ovalle; Tertiary.
- obesum*, *Cardium* – Philippi, 1887a: 178 [1887b: 171], pl. 39, fig. 11. Tubul, Chile; Hermann Volckmann; Tertiary. Holotype, SGO.PI.395 (n = 1).
- obliquatum*, *Cardium* – Philippi, 1887a: 175 [1887b: 169], pl. 39, figs. 1, 2, 2b, 14, *non* Michelotti, 1839, *non* Aradas, 1846. Hualpen, San Vicente & Algarrobo, Chile; Cretaceous. Syntypes, SGO.PI.282 (n = 1, from Hualpen, labeled as “lectotipo”); SGO.PI.285 (n = 1, from Hualpen, labeled as “paralectotipo”); SGO.PI.4770 (n = 1, from Hualpen, labeled as “paralectotipo”). Synonym of *Cardium (Rugicardium) acuticostatum* d'Orbigny, 1842 (Wilckens, 1904: 231–237, pl. 19, figs. 7–10), or as *C. (Bucardium) acuticostatum* d'Orbigny, 1842, Maastrichtian (Stinnesbeck, 1986: 174–175, pl. 3, figs. 1–5).
- obtusangulum*, *Cardium* – Philippi, 1887a: 175–176 [1887b: 169], pl. 39, fig. 4. Isla Quiriquina, San Vicente & Tomé, Chile; Cretaceous. Syntypes, SGO.PI.289 (n = 1, from Quiriquina, labeled as “lectotipo”); SGO.PI.389 (n = 1, from Quiriquina, labeled as “paralectotipo”); SGO.PI.619 (n = 1 valve, San Vicente); SGO.PI.620 (n = 1 valve, Tomé); SGO.PI.4771, 4773, 4774, 4775, 4777 (n = 1 valve each, from Quiriquina, labeled as “paralectotipo”). Synonym of *Cardium (Rugicardium) acuticostatum* d'Orbigny, 1842 (Wilckens, 1904: 231–237, pl. 19, figs. 7–10), or as *C. (Bucardium) acuticostatum* d'Orbigny, 1842, Maastrichtian (Stinnesbeck, 1986: 174–175, pl. 3, figs. 1–5).
- parvum*, *Cardium* – Philippi, 1844g: 39, 299, pl. 14, fig. 17a, 17b, *non* da Costa, 1778, *non*



- Mawe, 1823, *non* G. B. Sowerby II, 1841. Lago Fusaro, Naples, and Tarenti, Sicily, Italy. Bucquoy et al. (1892: 277, 282–283) proposed both *Parvicardium exiguum* var. *commutatum* and var. *scripta* as replacement names for *parvum* Philippi. Synonym of *Parvicardium exiguum* (Gmelin, 1791) (Sabelli et al., 1990: 310; Aartsen & Goud, 2000: 179, 181, 183; Hylleberg, 2004: 682–683) or as *P. exiguum commutatum* Bucquoy, Dautzenberg & Dollfus, 1892 (Janssen & Krylova, 2014: 63); type species (SD Crosse, 1885) of *Parvicardium* Monterosato, 1884.
- pencanum*, *Cardium* – Philippi, 1887a: 177 [1887b: 170], pl. 56, fig. 2. Hualpen, Chile; Cretaceous. Syntypes, SGO.PI.283 (n = 1, labeled as “lectotipo”); SGO.PI.4780 (n = 1 valve, labeled as “paralectotipo”). Synonym of *Cardium (Rugicardium) acuticostatum* d’Orbigny, 1842 (Wilckens, 1904: 231–237, pl. 19, figs. 7–10), or as *C. (Bucardium) acuticostatum* d’Orbigny, 1842, Maastrichtian (Stinnesbeck, 1986: 174–175, pl. 3, figs. 1–5).
- pisum*, *Cardium* – Philippi, 1887a: 179 [1887b: 172], pl. 39, fig. 9. Santa Cruz, Chile; Ramón Vidal Gormáz; Tertiary. Syntypes, SGO.PI.293 (n = 1 valve, labeled as “lectotipo”); SGO.PI.4785 (n = 1 valve, labeled as “paralectotipo”). *Cardium pisum* Philippi, 1887 (Ihering, 1907: 294).
- pulchellum*, *Cardium* – Philippi, 1844z4: 47, [86], pl. 2, fig. 8, *non* Gray, 1843. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Replacement name: *Cardium philippii* Deshayes, 1853 (Hylleberg, 2004: 695, 723). Synonym of *Parvicardium kochi* (Semper, 1861) (Janssen, 1979b: 100–101, pl. 3, fig. 52), but the Deshayes replacement name would be earlier.
- scabrum*, *Cardium* – Philippi, 1844g: 38, 299, pl. 14, fig. 16a, 16b. Sicily, Italy. The eastern Atlantic *Parvicardium scabrum* (Philippi, 1844) (Sabelli et al., 1990: 310; Aartsen & Goud, 2000: 179, figs. 25–27, 29; Hylleberg, 2004: 754; Huber, 2010: 301).
- sphaeridium*, *Cardium* – Philippi, 1887a: 179 [1887b: 172], pl. 28, fig. 6. Lebu, Chile; Tertiary. Syntypes, SGO.PI.296 (n = 1, labeled as “lectotipo”); SGO.PI.4783, 4784 (n = 1 each, labeled as “paralectotipo”).
- striatellum*, *Cardium* – Philippi, 1860a: 143–144 [1860b: 126], Petref. pl. 2, fig. 6. Desierto de Atacama, Chile; Tertiary.
- suave*, *Cardium* – Philippi, 1887a: 176 [1887b: 169–170], pl. 28, fig. 10. Hualpen, Chile; Cretaceous. Holotype, SGO.PI.284 (n = 1). Synonym of *Cardium (Bucardium) acuticostatum* d’Orbigny, 1842, Maastrichtian (Stinnesbeck, 1986: 174–175, pl. 3, figs. 1–5).
- subangulatum*, *Cardium* – Philippi, 1887a: 176 [1887b: 169], pl. 39, fig. 7, *non* Scacchi, 1836. Hualpen, Chile; Cretaceous. Syntypes, SGO.PI.621 (n = 1, labeled as “lectotipo”); SGO.PI.291, 4778, 4779 (n = 1 each labeled as “paralectotipo”). According to Cretella et al. (2005: 127), Scacchi’s species is a junior synonym of *Parvicardium exiguum* (Gmelin, 1791). Synonym of *Cardium (Rugicardium) acuticostatum* d’Orbigny, 1842 (Wilckens, 1904: 231–237, pl. 19, figs. 7–10), or as *C. (Bucardium) acuticostatum* d’Orbigny, 1842; Maastrichtian (Stinnesbeck, 1986: 174–175, pl. 3, figs. 1–5).
- tenuissimum*, *Cardium* – Philippi, 1887a: 179 [1887b: 172], pl. 39, fig. 10. No locality, Chile; Francisco J. Ovalle; Tertiary.
- vicentinum*, *Cardium* – Philippi, 1887a: 176–177 [1887b: 170], pl. 56, fig. 5. Tumbez Peninsula near San Vicente, Chile; Cretaceous. Syntype, SGO.PI.393 (n = 1 valve, San Vicente). Synonym of *Cardium (Rugicardium) acuticostatum* d’Orbigny, 1842 (Wilckens, 1904: 231–237, pl. 19, figs. 7–10), or as *C. (Bucardium) acuticostatum* d’Orbigny, 1842, Maastrichtian (Stinnesbeck, 1986: 174–175, pl. 3, figs. 1–5).
- volckmanni*, *Cardium* – Philippi, 1887a: 178–179 [1887b: 172], pl. 39, fig. 13. Lota, Chile; Volckmann; Tertiary. Holotype, SGO.PI.297 (n = 1 valve).

## Lahilliidae

- Amathusia* – Philippi, 1887a: 135 [1887b: 129], *non* Fabricius, 1807 [Lepidoptera], *non* Rafinesque, 1815 [Mecoptera], *non* Mulsant & Verreaux, 1866 [Aves]. Type species (SD Cossmann, 1898): *Amathusia angulata* Philippi, 1887, = *Corbis laevigata* G. B. Sowerby I, 1846. Tertiary, Chile. *Iheringia* Cossmann, 1899, *non* Keyserling, 1891 [Arachnida], *non* Lahille, 1898 [Echinodermata], *nom. nov. pro Amathusia* Philippi, 1887; *Lahillia* Cossmann, 1899, replacement name for both (Keen, 1969: N590).
- angulata*, *Amathusia* – Philippi, 1887a: 135–136 [1887b: 130], pl. 23, fig. 1, pl. 25, fig. 1; 1897: pl. 4. Navidad, Chile; José Toribio Medina; Tertiary [Miocene]. Syntypes, SGO.PI.431 (n = 1 valve, labeled as “lectotipo”); SGO.PI.435 (n = 2), SGO.PI.436 (n = 2 molds of SGO.PI.435), SGO.PI.4716 (n = 1) (all labeled as “paralectotipo”); plastotype,



MACN 4462 ("sent to Ihering by Philippi from Navidad, Chile") (Parodiz, 1996: 250). Synonym of *Lahillia laevigata* (G. B. Sowerby I, 1846) (Griffin & Nielsen, 2008: 270–272, pl. 7, figs. 8–11), which is the type species of *Lahillia* Cossmann, 1899.

*dorbignyi*, *Mactra* – Philippi, 1887a: 144 [1887b: 138], pl. 30, fig. 4. Isla Quiriquina, Chile; Cretaceous. Synonym of *Amathusia veneriformis* (Hupé, 1854) (Wilckens, 1904: 237–241, pl. 20, figs. 1–3), now *Lahillia veneriformis* (Hupé, 1854); Maastrichtian (Stinnesbeck, 1986: 175–176, pl. 3, figs. 6–7).

*ferrieri*, *Mactra* – Philippi, 1887a: 144 [1887b: 138], pl. 29, fig. 10. Isla Quiriquina, Chile; Cretaceous. Synonym of *Amathusia veneriformis* (Hupé, 1854) (Wilckens, 1904: 237–241, pl. 20, figs. 1–3), now *Lahillia veneriformis* (Hupé, 1854); Maastrichtian (Stinnesbeck, 1986: 175–176, pl. 3, figs. 6–7).

*orbicularis*, *Amathusia* – Philippi, 1887a: 136 [1887b: 130], pl. 24, fig. 1. Navidad; Tertiary [Miocene]. Holotype, SGO.PI.430 (n = 1 valve).

*pinguis*, *Mactra* – Philippi, 1887a: 144 [1887b: 138], pl. 31, fig. 5. Isla Quiriquina, Chile; Cretaceous. Synonym of *Amathusia veneriformis* (Hupé, 1854) (Wilckens, 1904: 237–241, pl. 20, figs. 1–3), now *Lahillia veneriformis* (Hupé, 1854), Maastrichtian (Stinnesbeck, 1986: 175–176, pl. 3, figs. 6–7).

*tumida*, *Mactra* – Philippi, 1887a: 144 [1887b: 138], pl. 30, fig. 3. Isla Quiriquina, Chile; Cretaceous. Synonym of *Amathusia veneriformis* (Hupé, 1854) (Wilckens, 1904: 237–241, pl. 20, figs. 1–3), now *Lahillia veneriformis* (Hupé, 1854); Maastrichtian (Stinnesbeck, 1986: 175–176, pl. 3, figs. 6–7).

#### Chamidae

*cancellata*, *Chama* – Philippi, 1836b: 228–229, 235 [pl. expl.], pl. 8, fig. 1. China Sea. Synonym of *Chama lobata* Broderip, 1835 (Huber, 2010: 283, 677).

*chilensis*, *Chama* – Philippi, 1887a: 180 [1887b: 173], pl. 37, fig. 9. Cahuil, Chile; Quaternary. Holotype, SGO.PI.632 (n = 1 valve) (Bernard, 1976: 20, 30, fig. 4d, who erroneously stated that the holotype was in the MNHN Paris). Synonym of *Chama pellucida* Broderip, 1835 (Bernard, 1976: 20, 30; Pastorino, 1991: 756; Nielsen, 2013: 56, figs. 11g–j).

*monstrosa* "?", *Chama squamosa* – Philippi, 1847-l: 54, pl. 8, fig. [not cited in text]. Magdeburg area, Germany; Tertiary; Sack's collection. The Oligocene *Chama monstrosa*

Philippi, 1847 (Glibert & Van de Poel, 1966a: 65).

#### Cyamiidae

*Cyamium* – Philippi, 1845i: 50–51. Type species (M): *Cyamium antarcticum* Philippi, 1845. Recent, Strait of Magellan, Chile (Smith, 1886; Huber, 2010: 263).

*antarcticum*, *Cyamium* – Philippi, 1845i: 51; 1847z6: 64–65, pl. 3, fig. 8. Gregory Bay, Strait of Magellan, Chile. Syntypes, MNHNS 227 (1 specimen); SMF 315699 (2 specimens + 4 valves) (largest, 17.8 mm x 9.7 mm); possible syntypes, ZMB 2050 (3 specimens + 3 valves). *Cyamium antarticum* Philippi, 1845 (Bernard, 1983: 33; Zelaya, 2016: 251).

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"Cyamiidae" / "Cyamioidea" – Some authors (e.g., Vokes, 1980: 115; Bernard, 1983: 33) have cited Philippi, 1845i as the source for this family-level name. However, this name was first used by G. O. Sars in 1878, as noted by Bouchet & Rocroi (2010: 32).

#### Gaimardiidae

*exilis*, *Phaseolicama* – Philippi, 1858b: 24. Islas Chonos, Chile; Fr. Fonk. Synonym of *Gaimardia trapesina* (Lamarck, 1819) (Bernard, 1983: 49).

#### Galeommatoidea sensu lato

*Arcinella* – Philippi, 1844g: 53–54, *non* Schumacher, 1817 [Chamidae]. Type species (SD Herrmannsen, 1846): "*Mytilus carinatus* Brocchi, 1814", as interpreted and figured by Philippi. Pliocene, Palermo, Sicily, Italy. The type species is not *Arcinella laevis* Philippi, 1844, as designated by Gray (1847: 190) one year later, which is an indeterminate species of *Kurtiella*. Italian paleontologists, such as Rossi Ronchetti (1951: 6) have concluded that Brocchi's *Mytilus carinatus* was based on a small specimen of Brocchi's (1814) own *Tellina revoluta*, which is now regarded as a corbulid. Glibert & Van de Poel (1966a: 51–52) classified the latter as *Caryocorbula revoluta* (Brocchi, 1814). However, what Philippi had in hand and figured (pl. 16, fig. 9) was not Brocchi's species, but rather a specimen of a species that would now be placed in the genus *Basterotia*. This situation is covered in ICZN Code Article 70.3 (1999)



- [Misidentified type species], which is specifically invoked here, as required by Article 70.3.2 (1999). Moreover, the name of this species of *Basterotia* also requires clarification. It is *Sphenia angulata* S. V. Wood, 1857, which was proposed in the synonymy of “*Saxicava ? carinata ?* Brocchi” (S. V. Wood, 1857: 289–290, pl. 29, fig 5a–e). This is the same species figured by Philippi. The name *angulata* has been accepted by later authors and placed variously in *Hiatella*, *Saxicava* or *Saxicavella*, starting with Monterosato (1874: 255), who specifically cited the material figured by Wood, which would then be its type material. A name proposed as a synonym is covered under ICZN Code Articles 11.6 and 72.4.3 (1999). Oliver (2013) recently transferred the Basterotiidae from the Cyamioidea to the Galeommatoidea.
- Bornia* – Philippi, 1836a: vii, 13–14; 1844g: 10–11; 1844z3: [1]. Type species (SD Stoliczka, 1870): *Bornia corbuloides* Philippi, 1836, ex Bivona ms; = *Cyclas sebetia* O. G. Costa, 1830. Pliocene-Recent, Europe (Huber, 2015: 488–489).
- Kellya* – Philippi, 1853a: 344–345, invalid emendation of *Kellia* Turton, 1822.
- Scacchia* – Philippi, 1844g: 27. Type species (SD Gray, 1847): *Tellina elliptica* Scacchi, 1833, non Brocchi, 1814; = *Lucina oblonga* Philippi, 1836. Recent, Mediterranean; the assignment of the subfamily Scacchiinae to a family remains uncertain (Huber, 2015: 504–505).
- anodon*, *Erycina* “?” – Philippi, 1836a: vii, 13, pl. 1, fig. 20. Palermo, Sicily, Italy; fossil. Possible syntype, PHB MB M.551 (L) 24 (n = 1) (missing in 2013). Synonym of *Tellimya ferruginosa* (Montagu, 1808) (Sabelli et al., 1990: 306). See also *Thracia elongata* Philippi, 1844g, five entries below.
- bullata*, *Kellia* – Philippi, 1845i: 51; 1860a: 175 [1860b: 157]. Cobija & Strait of Magellan, Chile. *Kellia bullata* Philippi, 1845 (Bernard, 1983: 31; Valdovinos, 1999: 155; Huber, 2015: 498; Zelaya, 2016: 252).
- complanata*, *Bornia* – Philippi, 1836a: vii, 14–15, pl. 14 [not cited in text]; 1844g: 10–11. Sicily, Italy. Fossil: Palermo “alteram ad Melazzo”. Possible syntypes, PHB MB M.541 (L) 24 (n = 1); PHB MB M.542 (L) 24 (n = 2) (missing in 2013). Synonym of “*Bornia*” *geoffroyi* (Payraudeau, 1826) (Sabelli et al., 1990: 304; Huber, 2015: 147, 489).
- coquimbana*, *Kellya* – Philippi, 1887a: 184 [1887b: 178], pl. 23, figs. 5, 7, “var. *major*”. Coquimbo & Cahuil, Chile; Quaternary.
- corbuloides*, *Bornia* – Philippi, 1836a: vii, 14, pl. 1, fig. 15, ex Bivona ms; 1844g: 11. Catania & Palermo, Sicily, Italy. Syntypes, SMF 315695 (Catania) (6 valves); ZMB 117921 Catania) (2 valves). Synonym of *Bornia sebetia* (O. G. Costa, 1830) (Sabelli et al., 1990: 304; Aartsen, 1996: 44, figs. 29L, 29R).
- elongata*, *Thracia* – Philippi, 1844g: 18; 1836a: pl. 1, fig. 20, non Roemer, 1841. Palermo, Sicily, Italy; fossil. The 1836 figure was that for his *Erycina anodon* Philippi, 1836a. Synonym of *Tellimya ferruginosa* (Montagu, 1808) (Sabelli et al., 1990: 306).
- grandis*, *Montacuta* – Philippi, 1887a: 185 [1887b: 178], pl. 23, fig. 3. Coquimbo, Chile; Quaternary. *Orobitella grandis* (Philippi, 1887) (Bernard, 1983: 32).
- inflata*, *Bornia* – Philippi, 1836a: vii, 14; 1844g: 11; 1844z3: [1]. Palermo & Trepani, Sicily, Italy. Also fossil “calcareo”; Palermo. Synonym of *Kellia suborbicularis* (Montagu, 1803), as suspected by Philippi (1844g) (Sabelli et al., 1990: 304; Kantor & Sysoev, 2005: 348).
- inversa*, *Scacchia* – Philippi, 1844g: 27–28, 299, pl. 14, fig. 10. Palermo, Sicily, Italy; fossil.
- laevis*, *Arcinella* – Philippi, 1844g: 54, 300, pl. 16, fig. 10. Palermo, Sicily, Italy; fossil. A species of *Kurtiella*, perhaps *K. bidentata* (Montagu, 1803) (Gofas & Salas, 2002: 122–125, figs. 5–8; Huber, 2015: 545). Erroneously regarded as the type species of *Arcinella* Philippi (q.v.).
- megalodon*, *Kellya* – Philippi, 1887a: 184 [1887b: 178], pl. 23, fig. 6. Coquimbo, Chile; Quaternary.
- miliaris*, *Kellia* – Philippi, 1845i: 51; 1860a: 175 [1860b: 157]. Eagle Bay, Strait of Magellan, Chile; E. B. Philippi. Syntypes SMF 315696 (Magellan) (n = 6); ZMB 2056 (Magellan) (n = 7). *Lasaea miliaris* (Philippi, 1845) (Carcelles & Williamson, 1951: 339; Reid & Osorio, 2000: 136, figs. 7H, 7I; Huber, 2015: 142, 503), not to be confused with *Kelliella miliaris* (Philippi, 1844), now in the Kelliellidae, *infra*.
- obliqua*, *Montacuta* – Philippi, 1887a: 185 [1887b: 178–179], pl. 23, fig. 4. Coquimbo, Chile; Quaternary.
- oblonga*, *Lucina* “?” – Philippi, 1836a: viii, 34, pl. 4, fig. 1 [not cited in text]. Trepani, Mondello & Palermo, Sicily, Italy. *Scacchia oblonga* (Philippi, 1836) (Sabelli et al., 1990: 305; Huber, 2015: 504).
- ovata*, *Scacchia* – Philippi, 1844g: 27, 299, pl. 14, fig. 9. Sicily, Italy. Syntype, ZMB 121036 (Sicily) (curated with the Donacidae).



*Scacchia ovata* Philippi, 1844 (Sabelli et al., 1990: 305), but more likely a *nomen dubium* (Aartsen, 1996: 53).

*parreyssii*, *Poronia* – Philippi, 1847r: 73. Australia; Parreyss. Synonym of *Lasaea australis* (Lamarck, 1818) (Hedley, 1915: 702; Huber, 2015: 502).

*pulchra*, *Kellia* – Philippi, 1849h: 149. West America. *Nomen dubium* (Coan & Valentich-Scott, 2012: 483), or *Cymatioa pulchra* (Philippi, 1849) (Bernard, 1983: 30).

*purpurata*, *Poronia* – Philippi, 1847r: 73. Australia; Parreyss. Synonym of *Lasaea australis* (Lamarck, 1818) (Hedley, 1915: 702) or a distinct species from New South Wales, *Lasaea purpurata* (Philippi, 1847) (Huber, 2015: 502).

*scalaris*, *Poronia* – Philippi, 1847r: 72–73. Australia; Parreyss. Synonym of *Lasaea australis* (Lamarck, 1818) (Lamprell & Healey, 1998: 156–157, fig. 410; Huber, 2015: 502).

*seminulum*, *Bornia* – Philippi, 1836a: vii, 14, pl. 1, fig. 16, 16a; 1844g: 11. Sicily, Italy. Syntypes, SMF 315697 (4 valves) (Sicily); ZMB 2056 (Sicily). Synonym of *Lasaea adansoni* (Gmelin, 1791) (Sabelli et al., 1990: 304), or of *L. rubra* (Montagu, 1803) because the west African *L. adansoni* is probably a separable species (Huber, 2015: 501).

*similis*, *Erycina* – Philippi, 1844g: 9, 299, pl. 13, fig. 8a–c. Lamati, Calabria, Italy; fossil.

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“*elliptica*, *Scacchia*” – Philippi, 1844g: 27. Although Philippi listed himself as author, this was merely the transfer of *Tellina elliptica* Scacchi, 1833, to *Scacchia*.

#### Glossidae

*sacki*, *Cypricardia* – Philippi, 1845z: 448 [*nomen nudum*]; 1847-l: 50–51, pl. 7, figs. 8a, b. Magdeburg area, Germany; Tertiary; Sack’s collection. *Miocardiopsis sacki* (Philippi, 1847) (R. Janssen, pers. comm., April 2013).

#### Kelliellidae

*miliaris*, *Venus* “?” – Philippi, 1844g: 36–37, 299, pl. 14, fig. 15a, 15b. Palermo, Sicily; fossil. Syntypes, NHMUK 1988056 (13 valves + 2 fragments) (redescribed by Allen, 2001: 201–203, figs. 1–3). *Kelliella miliaris* (Philippi, 1844), not to be confused with *Kellia miliaris* Philippi, 1845 (now in *Lasaea*, *supra*). This species has been listed as the senior syn-

onym of the type species of *Kelliella* M. Sars, 1870, *Kelliella abyssicola* M. Sars, 1870, and/or of *Kellia abyssicola* Forbes, 1844, which may be the same species and was published later in 1844 than that of Philippi (Janssen & Krylova, 2012: 91–92, pl. 2, figs. 6–9; Janssen & Krylova, 2014: 64), contrary to the analysis of Huber (2010: 706), as Huber (2015: 755) later admitted. The presence and biology of this species in the Recent fauna was discussed in detail by Clausen (1958).

#### Cyrenidae (formerly Corbiculidae)

*boliviana*, *Cyrena* – Philippi, 1851b: 70. Pacific Bolivia [prior to 1878, Bolivia’s territory extended westwards to the Pacific Ocean, now Chile?]; Largilliert. *Polymesoda* (*Neocyrena*) *boliviana* (Philippi, 1851) (Keen, 1971: 114, fig. 252; Bernard, 1983: 50), or as *Cyanocyclas boliviana* (Philippi, 1851) (Simone, 2006: 297, fig. 1035). However, no type material present at the Muséum de Rouen; locality definitely erroneous, as no cyrenids lived that far south in the 1850s. Thus a *nomen dubium* with an erroneous type locality (Huber, 2015: 798).

*buschii*, *Cyrena* – Philippi, 1849x: 78 [8], pl. 2, fig. 2. Locality unknown. Synonym of *Geloina coaxans* (Gmelin, 1791), from Asia and Australia (Huber, 2015: 799, 801).

*fontainei*, *Cyrena* – Philippi, 1851b: 70–71, *non* *Cyclas fontainei* d’Orbigny, 1846, a *Polymesoda* (Huber, 2015: 316). Locality unknown; Albers & Busch colls. Type material not located; *nomen dubium* (Huber, 2015: 798), or synonym of the eastern Pacific *Polymesoda* (*Egeta*) *altilis* (Gould, 1853) (Bernard, 1983: 50).

*gemmellarii*, *Cyrena* – Philippi, 1834b: 520 [*nomen nudum*]; 1836a: 39, pl. 4, fig. 3; 1844g: 31. Sicily, Italy: fossil in “argilla ad Defali prope Catania”. Possible syntypes PHB MB M.547 (M) 68 (n = 5) (missing in 2013). An extinct *Corbicula* (Huber, pers. commun., July 2013).

*inflata*, *Cyrena* – Philippi, 1851b: 71. Costa Rica; Busch coll. The Panamic brackish-water *Polymesoda inflata* (Philippi, 1851) (Bernard, 1983: 50; Ramírez et al., 2003: 269; Coan & Valentich-Scott, 2012: 467–468, pl. 155; Huber, 2015: 319, 793).

*largillierti*, *Cyrena* – Philippi, 1844z: 163; 1846d: 75 [1], pl. 1, fig. 1. Yang-tse River. China; Largilliert. Lectotype, ZMB 170.357a (36.6 mm x 33.1 mm), designated by Glaubrecht et al. (2007: 254–255, fig. 3C); para-



- lectotypes, ZMB 170.357b (2 non-matching valves); SMF 315418 (35.2 mm x 31.8 mm); MCZ 152932 (n = 2, ex Largilliert collection) (Johnson, 1959: 458); MCZ 152937 (n = 5, ex Largilliert); possible paralectotype MCZ 186474; paralectotype, MNHNS 50806 (missing as of 30 Oct. 2008); paralectotypes, Muséum de Rouen 142207003 (n = 5, largest, 41.1 mm x 36.8 mm). *Corbicula largillierti* (Philippi, 1844), from Asia (Prashad, 1929: 58–59, pl. 7, figs. 11–14), which has also been introduced into South America (Ituarte, 1994; Simone, 2006: 312, fig. 32; Huber, 2015: 303, 773).
- manilensis*, *Cyrena* – Philippi, 1844z: 162–163. Manila, Philippine Islands; Largilliert. Possible syntypes, Muséum de Rouen 142207005 (n = 4, largest is 36.4 mm x 33.9 mm, others slightly smaller, but these all may be larger than the measured specimen in the original description). *Corbicula manilensis* (Philippi, 1844), an often confused but valid *Corbicula* from the Philippine Islands and northern Borneo (Prashad, 1929: 64–65, pl. 8, figs. 10–12; Huber, 2015: 304, 777).
- nitens*, *Cyrena* – Philippi, 1844z: 163–164; 1846d: 76–77 [2–3], pl. 1, fig. 4. Yang-tse River, China; Largilliert. Syntypes, MNHNS 205 (n = 1 valve, 19.2 mm x 16.3 mm); MCZ 152933 (ex Largilliert collection) (18.1 mm x 15.3 mm); MCZ 186475 (20.1 mm x 17.2 mm) (Johnson, 1959: 458); Muséum de Rouen 142207042 (n = 8, largest, 20.9 mm x 18.3 mm). *Corbicula nitens* (Philippi, 1844), a valid Chinese *Corbicula* (Prashad, 1929: 59–60, pl. 7, figs. 15–19; Huber, 2015: 306, 773).
- pullata*, *Cyrena* – Philippi, 1850h: 110–111 [14–15]. Sumatra; Dinklage via Koch. Lectotype, ZMB 170.457a (27.0 mm x 26.2 mm), designated by Glaubrecht et al. (2007: 258–260, fig. 4A); paralectotype, ZMB 170.457b (23.4 mm x 21.6 mm); material may have come from Borneo; a valid *Corbicula* from Kalimantan and western Borneo, Sarawak; unknown from Sumatra (Prashad, 1930: 201–202, pl. 26, figs. 1–6; Huber, 2015: 306, 778).
- pusilla*, *Cyrena* – Philippi, 1846d: 78 [8], pl. 1, fig. 7, ex Parreyss ms. Nile River [Egypt / Sudan]. Syntypes, MNHNS 204 (n = 2, 10.9 mm x 9.2 mm; 6.9 mm x 5.6 mm); MCZ 154143 (n = 4) (ex Parreyss collection), MCZ 72899 (n = 6), and MCZ 197149 (n = 3) (ex Prime collection) (Johnson, 1959: 468, as “paratypes”) [MCZ 72899 and 197149 not seen; on loan to R. Kinzelbach since 1994]. Synonym of *Corbicula fluminalis consobrina* (Caillaud, 1827) (Daget, 1998: 170), or a valid species, *Corbicula (C.) pusilla* (Philippi, 1846), “widely distributed from N[orthern] Egypt – S[outh] Africa” (Huber, 2015: 307, 788).
- radiata*, *Cyrena* – Philippi, 1846d: 78 [8], pl. 1, fig. 8, ex Parreyss ms, *non* Hanley, 1845. Nile River, Bahr-el-abiad [Sudan]. Syntypes, MNHNS 50802 (n = 3, largest, 12.5 mm x 10.7 mm); MCZ 72900 (n = 4) and MCZ 154144 (n = 3) (ex Parreyss collection) (Johnson, 1959: 468, as “paratypes”) [MCZ syntypes not seen; on loan to R. Kinzelbach since 1994]. Synonym of *Corbicula fluminalis consobrina* (Caillaud, 1827) (Daget, 1998: 170). Pilsbry & Bequaert (1927: 341–343, figs. 71–72) noted that Philippi’s species, if used as a valid taxon, would require renaming due to *Cyrena radiata* Hanley, 1845 (eastern Pacific, now classified in *Polymesoda*), a senior homonym. Huber (2015: 307, 788) decided that “the identical *Cyrena pusilla* Philippi, 1846, is herein applied to represent this most common and widely distributed African *Corbicula* s.s.”
- solida*, *Cyrena* – Philippi, 1846d: 78–79 [4–5], pl. 1, fig. 9, *non* Dunker, 1843, a German fossil species. Nicaragua; Largilliert. Renamed as *Cyrena nicaraguana* Prime, 1869. Lectotype, MCZ 152935 (34.6 mm x 33.3 mm) (designated by Severeyn et al., 1994: 60–61); paralectotypes, Muséum de Rouen 142207004 (n = 2, 47.2 mm x 45.2 mm; 38.9 mm x 35.9 mm); MCZ 152935(b) (n = 1, 39.6 mm x 35.7 mm) (Johnson, 1959: 472; ex Largilliert collection); possible paralectotype, SMF 315420 (“America centr.”) (2 valves, 38.1 mm x 36.5 mm). However, Huber (2015: 796) rejected this lectotype designation, and regarded the two syntypes from Rouen as the only known type specimens. Severeyn et al. (1994) incorrectly listed Philippi’s junior homonym as an older name for the western Atlantic *Polymesoda (Neocyrena) arctata* (Deshayes 1855). Synonym of *Polymesoda (Neocyrena) fortis* (Prime, 1861), from the eastern Pacific (Coan et al., 2012: 472; Huber, 2015: 315, 796).

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“*suborbicularis*, *Cyrena*” – Busch, in Philippi, 1849x: 77 [7], pl. 2, fig. 1, *non* Melleville, 1843. Manila, Philippine Islands. The text is unlabeled as to author, and a discussion clearly written by Philippi indicated that the specimen was received from Busch. However, we think that the Latin description was prepared by his close collaborator Busch, who should be credited with the species



name. Synonym of *Geloina coaxans* (Gmelin, 1791), from Asia and Australia (Huber, 2015: 799).

### Sphaeriidae

*angulosa*, *Cyclas* – Philippi, 1858b: 23. Santiago, Chile.

*australe*, *Pisidium* – Philippi, 1836a: viii, 39; 1844g: 31, 299, pl. 14, fig. 11a, 11b. Sicily, Italy, freshwater. Syntypes, SMF 315357 (Panormo, ex Philippi) (n = 4 specimens). Woodward (1921: 209–210) concluded that this was an indeterminate, unidentifiable species, but the re-discovery of the type material may lead to its determination.

*carbonaria*, *Cyclas* – Philippi, 1887a: 158 [1887b: 152], pl. 23, fig. 2. Puchoco, Chile; Tertiary.

*colchaguensis*, *Cyclas* – Philippi, 1887a: 158 [1887b: 152], pl. 22, fig. 4. La Cueva, Colchagua, Chile; Tertiary [Pliocene].

*forbesii*, *Cyclas* – Philippi, 1869a: 41–42; Pfeiffer, 1869b: 489–490, pl. 105, figs. 15–17. Laguna Titicaca, Bolivia; David Forbes. *Sphaerium forbesii* (Philippi, 1869) (Kuiper & Hinz, 1984: 148–150; Ramírez et al., 2003: 273).

*auricochae*, *Cyclas* – Philippi, 1869a: 41; Pfeiffer, 1869b: 489, pl. 105, figs. 12–14. Laguna Lauricocha at the mouth of the Río Marañón, Amazonas, Peru. *Sphaerium auricochae* (Philippi, 1869) (Ramírez et al., 2003: 273). Neotype, SMF 186606 (Kuiper & Hinz, 1984: 150–154); “paraneotypes” SMF 186607 and ZMA/K 15483, but those specimens have no type status.

*phaseolina*, *Cyclas* – Philippi, 1887a: 159 [1887b: 153], pl. 25, fig. 2. Lebu, Chile; Tertiary.

*striata*, *Cyclas* – Philippi, 1887a: 158–159 [1887b: 152–153], pl. 25, fig. 4. Lebu, Chile; Jerman Volckmann; Tertiary.

*zonata*, *Cyclas* – Philippi, 1887a: 159 [1887b: 153], pl. 25, fig. 3. Lebu & Curauma, Chile; Tertiary. Syntypes, SGO.PI.489 (Curauma); SGO.PI.490 (n = 1 valve, Lebu, labeled as “lectotipo”); SGO.PI.4733–4742 (labeled as “paralectotipo”).

### Tellinidae

*algarrobensis*, *Tellina* – Philippi, 1887a: 136 [1887b: 130–131], pl. 26, fig. 14. Algarrobo, Chile; Ludwig Landbeck; Cretaceous. Holotype, SGO.PI.396 (n = 1 valve).

*ampullacea*, *Tellina* – Philippi, 1844-l: 125–126 [13–14], pl. 2, fig. 7. Senegal. Possible syntype, MNHNS 50413 (not found, March 2014); possible syntypes, Löbbecke Museum, Dusseldorf (Stoll, 2012: 23, fig.). The west African *Tellina ampullacea* Philippi, 1844, a senior synonym of *T. puella* Hanley, 1845 (Coan & Kabat, 2012: 314), as *Tamparella ampullacea* (Philippi, 1844) (Huber et al., in Huber, 2015: 626–627).

*angusta*, *Tellina tenuis* – Philippi, 1836a: 27, as “var.  $\beta$  [beta] *angusta*”; 1844g: 22, *non Tellina angusta* Gmelin, 1791. Locality? Syntypes, MNHNS 50377 (n = 5 specimens + 19 valves). *Nom. nov.*: *Macoma commutata* Monterosato, 1884. Synonym of *Macomangulus tenuis* (da Costa, 1778) (Huber, 2015: Chapter 5 on CD).

*anomala*, *Tellina* – Philippi, 1849i: 175, *non* Born, 1778. Locality unknown; Mörch. *Nomen dubium* (Huber et al., in Huber, 2015: Chapter 5 on CD).

*antonii*, *Tellina* – Philippi, 1844-l: 124 [12], pl. 2, figs. 3, 4. Locality unknown. Synonym of the western Atlantic *Tellinella mexicana* (Petit de la Saussaye, 1841) (Huber et al., in Huber, 2015: 577).

*araucana*, *Tellina* – Philippi, 1887a: 140 [1887b: 134], pl. 26, fig. 4. Tubul & Matanzas, Chile; Tertiary. Syntype, SGO.PI.424 (n = 1, from Matanzas, labeled as “holotipo”). *Tellina araucana* Philippi, 1887; Miocene (Frassinetti, 2004: 74, fig. 2).

*arcei*, *Tellina* – Philippi, 1887a: 138 [1887b: 132], pl. 27, fig. 3. Lebu, Chile; Tertiary. Syntypes, SGO.PI.401 (n = 1, labeled as “lectotipo”); SGO.PI.421 (n = 1 valve, labeled as “paralectotipo”); SGO.PI.4718, 4719 (n = 1 valve, each labeled as “paralectotipo”).

*auca*, *Tellina* – Philippi, 1887a: 141 [1887b: 135], pl. 26, fig. 19. Lebu, Chile; Tertiary. Holotype, SGO.PI.398 (n = 1 valve).

*birmanica*, *Tellina* – Philippi, 1849n: 55 [27], pl. 5, fig. 1. Mergui Archipelago, Burma [Myanmar]; Th. Philippi. Syntypes, SMF 315910 (Mergui) (n = 1) (56.5 mm x 38.4 mm); ZMB 3610 (Mergui) (n = 2) (58.5 mm x 41.1 mm; 59.0 mm x 36.8 mm); possible syntypes, Löbbecke Museum, Dusseldorf (Stoll, 2012: 23). The northern Indian Ocean *Austromacoma birmanica* (Philippi, 1849) (Dey, 2006: 66–67, pl. 29, fig. 3 [not 2 as in text], pl. 35, fig. 1; Huber et al., in Huber, 2015: 288–289, 736–737).

*brachyrrhyncha*, *Tellina* – Philippi, 1887a: 138 [1887b: 132–133], pl. 27, fig. 4. Lebu,



- Chile; Tertiary. Holotype, SGO.PI.400 (n = 1 valve).
- carbonaria*, *Tellina* – Philippi, 1887a: 137 [1887b: 131], pl. 26, fig. 18. Puchoco, Chile; Tertiary. Syntypes, SGO.PI.408 (n = 2 valves); SGO.PI.434 (n = 1 valve); SGO.PI.4717 (n = 1 valve), all labeled as “paralectotipo”.
- carnea*, *Tellina* – Philippi, 1844z: 162; 1846k: 91–91 [23–24], pl. 4, fig. 5, as a synonym of *Tellina iridescens*. Tschu-san [Zhousan], China; Largilliert. Syntype, MNHNS 242 (n = 1, 17.5 mm x 10.5 mm); SMF 315916 (1 valve) (China, ex Largilliert) (30.5 mm x 20.6 mm). Synonym of *Moerella iridescens* (Benson in Cantor, 1842) (Higo et al., 1999: 487), or as *Iridona iridescens* (Benson in Cantor, 1842) (Huber et al., in Huber, 2015: 214–215, 628–629).
- cicercula*, *Tellina* – Philippi, 1846h: 19. Mazatlán, Sinaloa, Mexico. MNHNS 50372 (n = 4 valves, but one is not conspecific; largest of the three is 11.4 mm x 7.6 mm). *Strigilla* (*Strigilla*) *cicercula* (Philippi, 1846) (Bernard, 1983: 42; Coan & Valentich-Scott, 2012: 621–622; Huber et al., in Huber, 2015: 265). Type species (OD) of *Roemerilla* Afshar, 1969, which is regarded as a synonym of *Strigilla* Turton, 1822.
- coarctata*, *Tellina* – Philippi, 1845w: 151. China. The southeast Asian *Leporimetis coarctata* (Philippi, 1845) (Swennen et al., 2001: 86, fig. 146, as *Florimetis*; Huber et al., in Huber, 2015: 275, 715). Dall (1909: 291) listed this as a junior synonym of *Tellina lacunosa* Dillwyn, 1817, which Dall erroneously attributed to “Hanley” and as being from “West Africa.”
- complanata*, *Tellina* – Philippi, 1887a: 137 [1887b: 131], pl. 26, fig. 12, *non* Gmelin, 1791. Algarrobo, Chile; Cretaceous. Possible syntype, SGO.PI.414 (n = 2 valves).
- concinna*, *Tellina* – Philippi, 1844-l: 123 [1], pl. 2, fig. 1. Locality unknown. Synonym of the western Atlantic *Laciolina laevigata* (Linnaeus, 1758) (Boss, 1966: 247–249, pl. 133, fig. 6, pl. 134, fig. 3, as *Tellina* (*Laciolina*); type locality “restricted” to Harrington Sound, Bermuda); Huber et al., in Huber, 2015: Chapter 5 on CD. Bernard (1983: 46) erroneously listed this as a junior synonym of the eastern Pacific *Psammotreta aurora* (Hanley, 1844).
- coquimbana*, *Tellina* – Philippi, 1887a: 142 [1887b: 136], pl. 26, fig. 6. Coquimbo, Chile; Quaternary. Syntypes, SGO.PI.407 (n = 1 valve, labeled as “lectotipo”); SGO.PI.409 (n = 1 valve); SGO.PI.4725–4729 (n = 1 valve each, all labeled as “paralectotipo”).
- costae*, *Tellina* – Philippi, 1834b: 519 [*nomen nudum*]; 1836a: vii, 28, pl. 3, fig. 11a, 11b; 1844g: 22. Catania, Sicily, & Cuma, Naples, Italy; Costa. Syntypes, SMF 315920 (Sicily) (n = 1) and SMF (uncat.) (n = 1) (34.2 mm x 23.2 mm). Synonym of *Macoma cumana* (O. G. Costa, 1830) (Priolo, 1973a: 74–76; Sabelli et al., 1990: 318–319), or as *Macomopsis cumana* (O. G. Costa, 1830) (Huber et al., in Huber, 2015: 721–722).
- crocea*, *Tellina donacina* var. – Philippi, 1836a: 25, as var. “concolor-rosea, flavescens, crocea ...” Locality presumably Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1898: 653), as *Tellina donacina* var. *crocea* Philippi, 1836. Synonym of *Moerella donacina* (Linnaeus, 1758) (Priolo, 1973a: 85).
- delicatula*, *Tellina* – Philippi, 1887a: 139 [1887b: 133], pl. 27, fig. 5, *non* Deshayes, 1855. Lebu, Chile; Tertiary. Holotype, SGO.PI.403 (n = 1 valve).
- dichotoma*, *Tellina* – Philippi, 1846h: 20. Mazatlán, Sinaloa, Mexico. *Strigilla* (*Strigilla*) *dichotoma* (Philippi, 1846) (Bernard, 1983: 42; Coan & Valentich-Scott, 2012: 621–622; Huber et al., in Huber, 2015: 265).
- dorbignyana*, *Tellina* – Philippi, 1887a: 139 [1887b: 133], pl. 25, fig. 10. Lebu, Chile; Tertiary.
- errazurizi*, *Tellina* – Philippi, 1887a: 140 [1887b: 134], pl. 26, fig. 15. Lebu, Chile; Tertiary. SGO.PI.406 (n = 1 valve, labeled as “paralectotipo”).
- ervilia*, *Tellina* – Philippi, 1846h: 20. Mazatlán, Sinaloa, Mexico. *Strigilla* (*Strigilla*) *ervilia* (Philippi, 1846) (Bernard, 1983: 42; Coan & Valentich-Scott, 2012: 623–624; Huber et al., in Huber, 2015: 266).
- flavescens*, *Tellina donacina* var. – Philippi, 1836a: 25, as var. “concolor-rosea, flavescens, crocea...” Locality presumably Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1898: 653), as *Tellina donacina* var. *flavescens* Philippi, 1836. Synonym of *Moerella donacina* (Linnaeus, 1758) (Priolo, 1973a: 85).
- foncki*, *Tellina* – Philippi, 1887a: 138 [1887b: 132], pl. 32, fig. 5. Lebu, Chile; Francisco J. Ovalle; Tertiary. Holotype, SGO.PI.418 (n = 1 valve).
- formosa*, *Tellina* – Philippi, 1887a: 137 [1887b: 131–132], pl. 27, fig. 1, *non* Hanley, 1844.



- Lebu, Chile; Tertiary. Syntypes SGO.PI.417 (n = 1 valve, labeled as "lectotipo"); SGO. PI.422 (possible syntypes).
- fricki*, *Tellina* – Philippi, 1887a: 139–140 [1887b: 133–134], pl. 26, fig. 5. Llancahue, Chile; Wilhelm Frick; Tertiary.
- gruneri*, *Tellina* – Philippi, 1845w: 150–151; 1849o: 56–57, pl. 5, fig. 3. Caribbean. Possible syntype, MNHNS 50441 (not found, March 2014). Synonym of the western Atlantic *Leporimetis intastriata* (Say, 1826) (Tryon, 1869: 105), or as *Leporimetis ephippium* (Spengler, 1798) (Huber et al., in Huber, 2015: 716–717).
- immaculata*, *Tellina* – Philippi, 1849o: 55–56 [27–28], pl. 5, fig. 2. Mergui Archipelago, Burma [Myanmar]; Th. Philippi. Possible syntype, MNHNS 50419 (not found, March 2014). The Indo-Pacific *Hanleyanus immaculatus* (Philippi, 1849) (Huber et al., in Huber, 2015: 223, 646–647).
- inconspicua*, *Tellina* – Philippi, 1887a: 140–141 [1887b: 134–135], pl. 26, fig. 8, *non* Broderip & G. B. Sowerby I, 1829. Lebu, Chile; Hermann Volckmann; Tertiary.
- jonasi*, *Tellina* – Philippi, 1847r: 74. Philippine Islands. Syntype, MNHNS 50440 (n = 1, 31.4 mm x 23.2 mm). The Philippine *Serratina jonasi* (Philippi 1847) (Huber et al., in Huber, 2015: 179, 587).
- landbecki*, *Tellina* – Philippi, 1887a: 136–137 [1887b: 131], pl. 26, fig. 11. Algarrobo, Chile; Cretaceous. Holotype, SGO.PI.157 (n = 1 valve).
- largillierti*, *Tellina* – Philippi, 1851c: 95. Gabon; Largilliert. Holotype, Muséum de Rouen 142204032 (79.0 mm x 54.1 mm). *Rostriacoma largillierti* (Philippi 1851), from West Africa (Huber et al., in Huber, 2015: 272, 707–708).
- lebuensis*, *Tellina* – Philippi, 1887a: 138 [1887b: 132], pl. 26, fig. 10. Lebu, Chile; Tertiary. Syntypes, SGO.PI.411 (n = 1, labeled as "lectotipo"); SGO.PI.397 (n = 1 valve); SGO. PI.423 (n = ? valve), SGO.PI.4720–4723 (all labeled as "paralectotipo"). *Tellina* (*Macoma*) *lebuensis* (Philippi, 1887); Miocene (Tavera, 1979: 85).
- lenticula*, *Tellina* – Philippi, 1846h: 19–20. Mazatlán, Sinaloa, Mexico. Synonym of *Strigilla* (*Strigilla*) *ervilia* (Philippi, 1846) (Bernard, 1983: 42; Coan & Valentich-Scott, 2012: 623–624).
- lima*, *Tellina* – Philippi, 1847r: 74–75. Basilan Island, China; Largilliert. Syntypes, MNHNS 50423 (n = 1, 29.5 mm x 21.0 mm); SMF 315946 (n = 5 valves) (largest, 11.8 mm x 9.9 mm). Synonym of *Serratina capsoides* (Lamarck 1818) (Boss, 1969b: 113, with *Serratina* as a subgenus of *Tellina*; Huber et al., in Huber, 2015: 587).
- macsporrani*, *Tellina* – Philippi, 1887a: 139 [1887b: 133], pl. 26, fig. 13. Lebu, Chile; MacSporran; Tertiary.
- mirabilis*, *Tellina* – Philippi, 1841b: 260–261; 1846h: 20. Locality not stated in 1841b; subsequently clarified as being southern U.S. and Cuba (1846h). The western Atlantic *Strigilla* (*Pisostrigilla*) *mirabilis* (Philippi, 1841) (Boss, 1969a: 362–365, pl. 165, fig. 3, pl. 169, fig. 1, pl. 171, fig. 1, type material not found; Mikkelsen & Bieler, 2007: 326; Tunnell et al., 2010: 372; Redfern, 2013: 411, fig. 1095; Huber et al., in Huber, 2015: 267, 701).
- ovalleana*, *Tellina* – Philippi, 1887a: 138 [1887b: 132], pl. 27, fig. 2. Isla Santa Maria, Chile; Tertiary. Holotype, SGO.PI.439 (n = 1 valve).
- panamensis*, *Tellina* – Philippi, 1849i: 175. Panama; E. B. Philippi. Syntypes, MNHNS 50405 (n = 1 specimen + 1 valve; largest, 26.6 mm x 20.5 mm). Synonym of *Psammotreta aurora* (Hanley, 1844) (Bernard, 1983: 46; Coan & Valentich-Scott, 2012: 612–613, pl. 188), or synonym of *Psammotreta psammotella* (Lamarck, 1818), a mislocalized Indo-Pacific species now regarded as being from the eastern Pacific (Huber et al., in Huber, 2015: 719–720).
- paula*, *Tellina* – Philippi, 1851c: 95–96. China; Largilliert. Syntype, MNHNS 50407 (n = 1, 10.8 mm x 9.6 mm). Synonym of the western Pacific *Abranda casta* (Hanley 1844) (Huber et al., in Huber, 2015: 686).
- pellucida*, *Tellina* – Philippi, 1843i: 72–73 [8–9], pl. 1, fig. 4, *non* Brocchi, 1814, *non* T. Brown, 1827. Locality unknown. Syntype, MNHNS 50472 (n = 1, 20.8 mm x 15.1 mm). Synonym of *Macomopsis retrorsa* (G. B. Sowerby II, 1867), which occurs from the Philippines to South Africa (Kilburn, 1973: 705), itself now a synonym of *Macomopsis moluccensis* (Martens, 1865) (Huber et al., in Huber, 2015: 724).
- philippii*, *Tellina* – Philippi, 1844-l: 126 [4], pl. 2, fig. 8, *ex* Anton ms. Locality unknown. Philippi signed this description himself, noting the name had come from Anton. The South African *Tellinella philippii* (Philippi, 1844) (Kilburn, 1974: 347; Coan & Kabat, 2012: 314; Huber et al., in Huber, 2015: 171, 574, type locality "clarified to Tanzania").



*platensis*, *Tellina* – Philippi, 1893b: 9, pl. 1, fig. 6. Argentina; Tertiary. “*Tellina*” *platensis* Philippi, 1893, Miocene (Ihering, 1907: 387; del Río & Martínez, 1998: 70, pl. 19, fig. 8).

*pleurosticta*, *Tellina* – Philippi, 1836a: vii, 30; 1844g: 23. Militello, Sicily, Italy; fossil in “tufo basaltico”. Possible syntype, PHB MB M.537 (VI) 25 (n = 1) (missing in 2013).

*promaucana*, *Tellina* – Philippi, 1887a: 141–142 [1887b: 136], pl. 26, fig. 9. Navidad, Chile; Tertiary [Miocene].

*pusilla*, *Tellina* – Philippi, 1836a: vii, 29, pl. 3, fig. 9a, 9b; 1844g: 23, *non* Gmelin, 1791, *non* Lamarck, 1806. Palermo, Sicily, Italy; fossil “calcareo”. Possible syntypes PHB MB M.536 (VI) 28 (n = 2) (missing in 2013). Synonym of *Tellina pygmaea* Lovén, 1846 (Sabelli et al., 1990: 317), or as *Asbjornsenia pygmaea* (Lovén, 1846) (Huber et al., in Huber, 2015: 676). Philippi (1841f: 8; 1844z4: 8, 45) also reported his species from German fossil outcrops now known to be Oligocene, but this material is unlikely to be conspecific. Cosel (1995: 58–59) determined that the tropical eastern Atlantic records of this species are instead *Tellina* (*Moerella*) *pseudopusilla* Cosel, 1995.

*striatella*, *Tellina* – Philippi, 1887a: 140 [1887b: 134], pl. 26, fig. 3. Navidad, Chile; Tertiary [Miocene]. Syntype, SGO.PI.404 (n = 1, labeled as “lectotipo”).

*strigilata*, *Tellina* – Philippi, 1844g: 23–24, pl. 14, fig. 6, *non* Spengler, 1798. Palermo, Sicily; fossil. Syntype, MNHNS 241 (n = 1 valve, 42.2 mm x 27.6 mm). Synonym of *Tellina compressa* Brocchi, 1814 (Sabelli et al., 1990: 317), or as *Oudardia compressa* (Brocchi, 1814) (Huber et al., in Huber, 2015: 661).

*strigilata*, *Tellina* – Philippi, 1847r: 75; 1849o: 57 [29], pl. 5, fig. 4, *non* Spengler, 1798, *non* Philippi, 1844g. Locality unknown. Synonym of the eastern Pacific *Temnoconcha cognata* (C. B. Adams, 1852) (Huber et al., in Huber, 2015: 648).

*subfalcata*, *Tellina* – Philippi, 1887a: 137 [1887b: 131], pl. 26, fig. 17. Puchoco, Chile; Hermann Volckmann; Tertiary. Syntypes, SGO.PI.405 (n = 1 valve, labeled as “lectotipo”); SGO.PI.438 (n = 1 valve, labeled as “paralectotipo”). Both syntype lots are labeled as from Lota; Puchoco is part of, or adjacent to Lota.

*sulcata*, *Tellina* – Philippi, 1836b: 226–227, 235 [pl. expl.], pl. 7, fig. 3, *non* Solander in Brander, 1766, *non* W. Wood, 1815. Manila,

Philippine Islands. *Nomen dubium*, possibly non-tellinoid (Huber et al., in Huber, 2015: Chapter 5 on CD).

*tenuicula*, *Tellina* – Philippi, 1887a: 141 [1887b: 135], pl. 26, fig. 7. Navidad; Tertiary [Miocene]. Syntypes, SGO.PI.399 (n = 1 valve); SGO.PI.4724 (n = 1 valve); both lots labeled as “paralectotipo”. *Psammotreta tenuicula* (Philippi, 1887), which also occurs in the Pliocene (Frassinetti, 1997: 73, 70–71, pl. 2, figs. 7, 8).

*tubulensis*, *Tellina* – Philippi, 1887a: 140 [1887b: 134], pl. 32, fig. 7. Tubul, Chile; Tertiary. The Pliocene *Macoma tubulensis* (Philippi, 1887) (Frassinetti, 1997: 72–73, 70–71, pl. 2, fig. 6), or junior synonym of *Macoma inornata* (Hanley, 1844), Pliocene to Recent (Nielsen & Valdovinos, 2008: 206, fig. 9); now *Macoploma inornata* (Hanley, 1844) (Huber et al., in Huber, 2015: 731).

*volckmanni*, *Tellina* – Philippi, 1887a: 139 [1887b: 133], pl. 32, fig. 2. Lebu, Chile; Volckmann; Tertiary. Possible syntype, SGO.PI.420 (n = 1, labeled as “paralectotipo?”), but from Tubul, which is very close to Lebu.

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“*meyeri*, *Tellina*” – Philippi, 1846k: 89–90 [21–22], pl. 4, fig. 1. This species was listed by Higo et al. (1999: 490) and by Qi (2004: 282, as “1847”) as by Philippi, but the description was signed by Dunker (with the addition of a note by Philippi) (Huber et al., in Huber, 2015: 711. Type species of *Apolymetis* Salisbury, 1929.

“*natalensis*, *Tellina*” – Philippi, 1846k: 91 [23], pl. 4, fig. 4. This species was listed by Boss (1969b: 131–133) as by Philippi, but the description was signed by Krauss. *Nitidotellina natalensis* (Krauss in Philippi, 1846) (Huber et al., in Huber, 2015: 653, 655).

“*truncata*, *Tellina*” – Philippi, 1843i: 71–72 [7–8], pl. 1, fig. 2. This species was listed as by Philippi in Higo et al. (1999: 490), but the description was signed by Jonas, so it should be listed as Jonas in Philippi; now a synonym of *Psammacoma gubernaculum* (Hanley, 1844) (Huber et al., in Huber, 2015: 724, 729).

#### Donacidae

*Amphichaena* – Philippi, 1847z6: 63. Type species (M): *Amphichaena kindermanni* Philippi, 1847. Recent, Panamic province.



*angusta*, *Donax* – Philippi, 1849h: 145–146. Locality unknown; Largilliert. Syntype, MNHNS 50459 (n = 1, 24.2 mm x 12.5 mm).

*chemnitzii*, *Galatea* – Philippi, 1850-l: 124 [2]. Based on figures in Chemnitz (1795: pl. 202, figs. 1985 & 1986). An unresolved species of *Galatea*, most similar to *G. laeta* Philippi, 1849 (Huber, 2010: 693). These same Chemnitz figures were mistakenly cited by G. B. Sowerby I (1825: 12) for his *Donax aequilatera*, whereas he had intended to cite figs. 1983 and 1984, corresponding to Chemnitz' *Venus donacina*; the latter had already been made available by Megerle von Mühlfeld, 1811, ex Chemnitz ms, a species now placed in *Macridiscus* (Huber, 2015: 763).

*hanleyanus*, *Donax* – Philippi, 1847r: 84–85, as *D. "hanleyana"*. Locality unknown. Junior synonym of *Donax hilairea* Guérin, 1832, but conserved as the western Atlantic *Donax hanleyanus* Philippi, 1847, by ICZN Opinion 1372 (ICZN, 1986) (Narchi, 1983; Narchi, 1989: 305–310, figs. 1, 2; Rios, 1994: 279–280, pl. 96, fig. 1371; Huber, 2010: 313).

*kindermanni*, *Amphichaena* – Philippi, 1847z6: 63–64, pl. 3, fig. 7. Mazatlán, Mexico; Kindermann. Type species of *Amphichaena* Philippi, 1847. The Panamic *Donax* (*Amphichaena*) *kindermanni* (Philippi, 1847) (Coan & Valentich-Scott, 2012: 666–667, pl. 204).

*laeta*, *Galatea* – Philippi, 1849p: 190; 1850-l: 123–124 [1–2], pl. 1, fig. 2. Locality unknown. The Angolan freshwater *Galatea laeta* Philippi, 1849 (Huber, 2010: 322).

*lunularis*, *Donax* – Philippi, 1847r: 77. Locality unknown. The NHMUK type collection has two valves labeled as "type" (without catalog number), but these are merely the specimens figured by Reeve (1854, pl. 4, fig. 20), which Römer (1870: 33) soon recognized was an entirely different species from that described by Philippi.

*obesa*, *Donax* – Philippi, 1851c: 75, *non* d'Orbigny, 1846. California. Synonym of the Californian-Panamic *Donax gouldii* Dall, 1921 (Bernard, 1983: 49; Coan & Valentich-Scott, 2012: 677–678, pl. 209).

*panamensis*, *Donax* – Philippi, 1849h: 145. Panama; E. B. Philippi. Synonym of the Panamic *Donax* (*Assimilidonax*) *assimilis* Hanley, 1845; NHMUK 1952.10.30.93, lectotype (designated by Coan, 1983: 281–282, figs. 17–19); redescribed by Coan & Valentich-Scott (2012: 675–676, pl. 208); paralectotypes SMF 315474 (n = 3).

*parvula*, *Donax* – Philippi, 1849h: 146. Florida"?; Largilliert. Synonym of *Donax fossor* Say, 1822, or a valid species, *Donax (Paraserrula) parvulus* Philippi, 1849 (Huber, 2015: 746).

*pusilla*, *Donax* – Philippi, 1849h: 146. Senegal; Largilliert. Syntype, MNHNS 51831 (n = 1, 20.9 mm x 11.9 mm). The west African *Donax pusillus* Philippi, 1848 (Huber, 2010: 313, 690).

*roemeri*, *Donax* – Philippi, 1849h: 147; 1849z5: 452–453. Galveston, Texas; Römer. Synonym of *Donax variabilis* Say, 1822 (Tunnell et al., 2010: 373–374).

*rubicunda*, *Galatea* – Philippi, 1849p: 190–191; 1850-l: 123 [1], pl. 1, fig. 1. Locality unknown. The Angolan freshwater *Galatea rubicunda* Philippi, 1849 (Huber, 2010: 322).

*securiformis*, *Donax* – Philippi, 1845i: 53. "New Zealand?". Not from New Zealand (B. Marshall, pers. comm., May 2013).

*sulcata*, *Donax* – Philippi, 1847r: 76. Locality unknown.

*tenuicula*, *Galatea* – Philippi, 1849q: 191; 1850-l: 124 [2], pl. 1, fig. 3. Locality not stated.

*texasiana*, *Donax* – Philippi, 1847r: 77; 1849z5: 452. Galveston, Texas. Syntypes, MNHNS (no number) (n = 2, larger, 12.7 mm x 10.7 mm). The western Atlantic *Donax texasianus* Philippi, 1847 (Huber, 2010: 316; Tunnell et al., 2010: 373).

*tumida*, *Donax* – Philippi, 1849h: 147; 1849z5: 453. Galveston, Texas; [Römer]. Synonym of *Donax texasianus* Philippi, 1847.

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"*Galatea* – Philippi, '1850'." Dodge (1947: 487), who incorrectly rejected most of the names established in Bruguière (1797), and Neave (1939: 432), stated that Philippi (i.e., 1850-l: 123) was the "first valid proposal" of this genus name. (Philippi's first use of this generic name was actually in 1849q.) However, subsequent authors recognized that this name did, in fact, date from Bruguière, 1797.

#### Icanotiidae

*crispa*, *Icanotia* "?" – Philippi, 1899: 98, pl. 35, fig. 9, 9a. Atacama, Chile; Eduardo Lira; [Mesozoic].

*laeviuscula*, *Icanotia* "?" – Philippi, 1899: 98, pl. 35, fig. 10, 10a. Locality unknown, Chile; [Mesozoic].



## Psammobiidae

*angusta*, *Psammobia* – Philippi, 1841f: 7; 1844z4: 7, [86], pl. 2, fig. 6. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Gari* (*Psammotaena*) *angusta* (Philippi, 1841) (Janssen, 1979b: 114–116, pl. 3, fig. 60, who dated the species from 1843). Type material lost (R. Janssen, pers. comm., April 2013).

*bipartita*, *Psammobia* – Philippi, 1849i: 166. Manila, Philippine Islands; Largilliert. Syntype, MNHNS 198 (n = 2 valves, 35.6 mm x 20.4 mm) (Willan, 1993: 15 stated that the type material was “originally in Largilliert coll. ... Rouen, France, but it cannot be located there and is presumed lost”). Synonym of *Gari* (*Gari*) *truncata* (Linnaeus, 1767) (Willan, 1993: 14–17, figs. 1, 2, 38–48; Higo et al., 1999: 493).

*darwinii*, *Psammobia* “?” – Philippi, 1887a: 142 [1887b: 136], pl. 16, fig. 16. Mouth of Río Rapel, Chile; Tertiary. *Psammobia darwini* Philippi, 1887 (Ihering, 1907: 351), or a synonym of *Psammobia patagonica* Philippi, 1887 (Feruglio, 1937: 179–180).

*discors*, *Psammobia* – Philippi, 1836a: vii, 23, pl. 3, fig. 8. Palermo, Sicily, Italy. Possible syntype, MNHNS 210 (n = 1, missing in March 2014). Synonym of *Gari costulata* (Turton, 1822) (Sabelli et al., 1990: 321).

*patagonica*, *Psammobia* – Philippi, 1887a: 143 [1887b: 137], “pl. 26, fig. 17”. Santa Cruz, Chile; Ramón Vidal Gormáz; Tertiary. *Psammobia patagonica* Philippi, 1887 (Ihering, 1907: 311–312; Feruglio, 1937: 179–180), although Steinmann & Wilckens (1908: 47–49) transferred this to *Mactra* [Mactridae]; further study is required.

*solida*, *Psammobia* – Philippi, 1844e: 97 [1], pl. 1, fig. 1; 1860a: 175 [1860b: 157], *non* J. Sowerby, 1822 [Eocene, Great Britain]. Isla Chiloe, Chile; E. B. Philippi. Syntypes, SMF 316009 (3 valves) (not found, Sept. 2013). Synonym of the commercially important Peruvian and Chilean *Gari solida* (Gray, 1828) (Güller & Zelaya, 2016a: Supplementary Materials, at 7). There is no evidence that Philippi knew of Gray’s species, originally described in the genus *Solen*, and he coincidentally selected the same species name.

*striatella*, *Psammobia* – Philippi, 1849i: 166–167. Locality unknown. Syntype, MNHNS 223 (n = 1 valve, 23.8 mm x 21.1 mm); Willan (1993: 17) noted that no type material was extant in ZMB or SMF. Synonym of *Gari*

(*Gari*) *lessoni* (Blainville, 1826) (Willan, 1993: 17–19, figs. 4, 5, 49–54).

*ventricosa*, *Sanguinolaria* – Philippi, 1851c: 94–95. Locality unknown; Largilliert. Holotype, Muséum de Rouen 142205016 (38.9 mm x 26.3 mm). Synonym of *Asaphis violascens* (Forsskal in Niebuhr, 1775) (Huber, 2010: appendix).

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“*radiata*, *Psammobia*” – Philippi, 1845c: 194 [4], pl. 2, fig. 5. This species was listed by Prashad (1932: 300), Scarlato (1965: 51) and Qi (2004: 291) as by Philippi, but the description was signed by Dunker. *Gari* (*Psammobia*) *radiata* (Dunker in Philippi, 1845) (Willan, 1992).

## Semelidae

*antiqua*, *Cumingia* “?” – Philippi, 1887a: 158 [1887b: 151–152], pl. 23, fig. 10. Lebu, Chile; Volckmann; Tertiary.

*carbonaria*, *Semele* “?” – Philippi, 1887a: 157 [1887b: 151], pl. 23, fig. 15. Lebu, Chile; Tertiary. Syntypes, SGO.PI.462 (n = 1 valve, labeled as “lectotipo”); SGO.PI.4730 (n = 1 valve, labeled as “paralectotipo”).

*deforme*, *Amphidesma* – Philippi, 1849h: 129–130; 1849z5: 452. Galveston, Texas. Huber et al., in Huber (2015: Chapter 5 on CD) indicated that this is probably a *nomen dubium* of *Abra*, with *Abra lioica* (Dall, 1881) as the first available name for the Gulf of Mexico species.

*obliquata*, *Semele* – Philippi, 1887a: 156–157 [1887b: 150], pl. 23, fig. 12. Between Puchoco & Lota, Chile; Hermann Volckmann; Tertiary. Holotype, SGO.PI.461 (n = 1).

*ovata*, *Erycina* – Philippi, 1836a: vii, 13, pl. 1, fig. 13, *non* Gray, 1825; 1844g: 8–9. Sicily, Italy. Synonym of *Abra segmentum* (Récluz, 1843) (Sabelli et al., 1990: 322; Kantor & Sysoev, 2005: 362). Philippi’s taxon is the type species (SD Crosse, 1885) of *Lutricularia* Monterosato, 1884, a synonym of *Abra* Lamarck, 1818.

*pusilla*, *Erycina* – Philippi, 1836a: vii, 13, pl. 1, fig. 5; 1844g: 9. Palermo, Sicily, Italy; fossil “calcareo”. Synonym of *Ervilia castanea* (Montagu, 1803) (Sabelli et al., 1990: 315).

*tenuis*, *Scrobicularia* – Philippi, 1844g: 8, 299, pl. 14, fig. 7. Palermo, Sicily; fossil. Synonym of *Abra nitida* (O. F. Müller, 1776) (Sabelli et al., 1990: 322); Philippi’s taxon is the type species (M) of *Limicola* Gray, 1857,



*non* Koch, 1816 [Aves], *non* Gray, 1852, ex Leach ms [Tellinidae], which is regarded as a synonym of *Abra* Lamarck, 1818.

#### Solecurtidae

*exaratus*, *Solen* – Philippi, 1849i: 174. Locality unknown. The western Pacific *Solecurtus exaratus* (Philippi, 1849) (Huber, 2010: 347, 703).

#### Mactridae

*adansonii*, *Mactra* – Philippi, 1849i: 152. Guinea and Senegal. Syntype, MNHNS 51609 (n = 1, 39.7 mm x 29.9 mm).

*ambigua*, *Mactra* – Philippi, 1887a: 146–147 [1887b: 140–141], pl. 27, fig. 11. Hualpen, Chile; Pedro Lucio Cuadra; Cretaceous & also a figure in d'Orbigny. Synonym of *Mactra araucana* d'Orbigny, 1842 (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).

*amphirrhyncha*, *Mactra* – Philippi, 1887a: 147 [1887b: 141], pl. 32, fig. 15. Isla Quiriquina, Chile; Cretaceous. Synonym of *Mactra araucana* d'Orbigny, 1842 (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).

*angustior*, *Lutraria elliptica* – Philippi, 1844g: 7. Sicily, Italy. The eastern Atlantic *Lutraria angustior* Philippi, 1844 (Sabelli et al., 1990: 314; Giribet & Peñas, 1997: 58 [20]; Huber, 2010: 450).

*apicina*, *Mactra* – Philippi, 1887a: 152 [1887b: 145–146], pl. 29, fig. 3. Navidad, Chile; Tertiary [Miocene].

*araucana*, *Lutraria* – Philippi, 1887a: 164 [1887b: 158], pl. 34, fig. 3. Puchoco, Matanzas, and mouth of Río Rapel, Chile; Tertiary. Syntypes, SGO.PI.365 (n = 1 valve, Boca Rio Rapel); SGO.PI.368 (n = 1 valve, Puchoco, labeled as “holotipo”); SGO.PI.371 (n = 1 valve, Matanzas).

*biangulata*, *Mactra* – Philippi, 1887a: 152 [1887b: 146], pl. 27, fig. 17. Puchoco, Chile; Volckmann; Tertiary.

*bonariensis*, *Mactra* – Philippi, 1893b: 8–9, pl. 1, fig. 5. Argentina; Tertiary. Neotype, MAS-Pi 067 (La Juanita, Entre Rios, Argentina; Paraná Formation, late Miocene), designated by Pérez & Signorelli (2011: 597, figs. 2A, 2B). *Mactra bonariensis* Philippi, 1893 (Ihering, 1907: 387; del Río & Martínez, 1998: 69, pl. 19, fig. 7).

*brevicula*, *Lutraria* – Philippi, 1887a: 165 [1887b: 159], pl. 33, fig. 7. Lebu, Chile; Tertiary. Holotype, SGO.PI.373 (n = 1).

*calbucana*, *Mactra* – Philippi, 1893a: 9, pl. 2, fig. 5. Calbuco, Reloncaví, Chile. Holotype, MNHNS 232 (69.8 mm x 52.4 mm) (Signorelli & Pastorino, 2011: figs. 11h–11i). Junior synonym of *Mulinia byronensis* Gray, 1837 (Dall, 1909: 286; Bernard, 1983: 40, but erroneously listed again under *Tivela byronensis* (Gray, 1838) in the Veneridae, (Bernard, 1983: 53), or of *Mulinia exalbida* Gray, 1837 (Signorelli & Pastorino, 2011: 58–60, figs. 11–12; Huber, 2015: 836).

*carbonaria*, *Mactra* – Philippi, 1887a: 151 [1887b: 145], pl. 30, fig. 5. Puchoco, Chile; Volckmann; Tertiary.

*cecillii*, *Mactra* – Philippi, 1849r: 26. Bali; Largilliert. Syntypes, MNHNS 51628 (n = 2, largest 30.8 mm x 22.8 mm); the lot in Muséum de Rouen labeled as this species (142209026) is actually a *Macoma* (Tellinidae). *Nomen dubium* (Huber, 2010: 754).

*chemnitzii*, *Lutraria* – Philippi, 1849r: 26. East Indies; Liewkiew Island [Ryukyu Islands, Japan]; Largilliert. Synonym of the Indo-Pacific *Meropesta nicobarica* (Gmelin, 1791).

*chinensis*, *Mactra* – Philippi, 1846c: 73 [7]. China. Syntype, SMF 316252 (n = 1) (48.1 mm x 38.0 mm); possible syntype, MNHNS 51632 (not found in March 2014). The western Pacific *Mactra chinensis* Philippi, 1846 (Abbott & Dance, 1982: 334; Higo et al., 1999: 476; Okutani, 2000: 962–963, fig. 1; Qi, 2004: 268, pl. 148E; Kantor & Sysoev, 2005: 393; Huber, 2010: 439; Lutaenko, 2014), although further study is needed to resolve the taxa in the Sea of Japan (Reunov et al., 2014).

*cibaria*, *Mactra* – Philippi, 1893a: 9, pl. 1, fig. 4. Strait of Magellan, Chile. Holotype, MNHNS 206 (73.4 mm x 57.3 mm) (Signorelli & Pastorino, 2011: figs. 11e–11g). Synonym of *Mulinia edulis* (King, 1832) (Dall, 1909: 286), or of *Mulinia exalbida* Gray, 1837 (Signorelli & Pastorino, 2011: 58–60, figs. 11–12).

*colossea*, *Mactra* – Philippi, 1887a: 143 [1887b: 137], pl. 28, fig. 1, pl. 29, fig. 2. Isla Quiriquina & Tumbes Peninsula near San Vicente, Chile; Tomé; Edmundo Larenas; Cretaceous. *Mactra colossea* Philippi, 1887 (Wilckens, 1904: 261–263, pl. 20, figs. 8–9; Wetzel, 1930: 80), or *Mulinoides colossea* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 177, pl. 4, fig. 9).

*conchae*, *Mactra* – Philippi, 1887a: 145–146 [1887b: 139–140], pl. 29, fig. 5. Tomé, Chile; Enrique Concha; Cretaceous. Synonym of *Mactra araucana* d'Orbigny, 1842 “?” (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).



- coquimbana*, *Macra* – Philippi, 1887a: 254, 263 [1887b: 244, 353], pl. 30, fig. 2; 1893a: 10, pl. 2, fig. 7. Coquimbo, Chile. Holotype, MNHNS 212 (58.9 mm x 48.7 mm) (Signorelli & Pastorino, 2011: figs. 8i–8k). Synonym of *Mulinia byronensis* Gray, 1837 (Dall, 1909: 287), or of *Mulinia edulis* (King, 1832) (Signorelli & Pastorino, 2011: 55–58, figs. 8–10), or a valid species of *Mulinia* (Bernard, 1983: 40), but erroneously listed again under *Tivela byronensis* (Gray, 1838) in the Veneridae (Bernard, 1983: 53).
- corbicula*, *Macra* – Philippi, 1851c: 80. Liewkiew Island, China [Ryukyu Islands, Japan]; Cécille via Largilliert. *Nomen dubium* (Huber, 2010: 754).
- cuadrae*, *Macra* – Philippi, 1887a: 145 [1887b: 139], pl. 29, fig. 4. Hualpen, Chile; Cretaceous. Synonym of *Macra araucana* d'Orbigny, 1842 (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).
- cuadrae*, *Venus* – Philippi, 1887a: 119 [1887b: 113], pl. 19, fig. 5. Hualpen, Chile; Cretaceous. Synonym of *Macra araucana* d'Orbigny, 1842 (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).
- cygnea*, *Macra* – Philippi, 1844z: 161–162; 1846c: 74 [8], *non* Spengler, 1802. Red Sea. Philippi (1846c: 74 [8]) recognized the homonymy of his earlier taxon, and concluded that *Macra olorina* Philippi, 1846, was available for this species (Sabelli et al., 1990: 313, as “*M. cygnaea*” having overlooked the homonymy).
- dubia*, *Macra* – Philippi, 1887a: 147 [1887b: 141], pl. 27, fig. 6, *non* J. Sowerby, 1817. Isla Quiriquina; Cretaceous. Synonym of *Macra araucana* d'Orbigny, 1842 (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).
- eburnea*, *Macra* – Philippi, 1849s: 27. Liewkiew Island [Ryukyu Islands, Japan]; Largilliert. Syntype, MNHNS 51626 (n = 2 valves, 25.5 mm x 22.2 mm). The western Pacific *Macra eburnea* Philippi, 1849 (Huber, 2010: 440, 755).
- egregia*, *Venus* – Philippi, 1887a: 117 [1887b: 111], pl. 18, fig. 2. Hualpen, Chile; Cretaceous. Holotype, SGO.PI.167 (n = 1 valve). Synonym of *Mulinoides colossea* (Philippi, 1887), Cretaceous (Stinnesbeck, 1986: 177, pl. 4, fig. 9).
- epidermia*, *Macra* – Philippi, 1893a: 9, pl. 1, fig. 3, *non* Deshayes in Reeve, 1854. Strait of Magellan, Chile. Holotype, MHNHS 219 (57.0 mm x 43.7 mm) (Signorelli & Pastorino, 2011: figs. 2i–2l). Synonym of *Mulinia edulis* (King, 1832) (Dall, 1909: 286; Bernard, 1983: 40), or of *Macra fuegiensis* Smith, 1905 (Signorelli & Pastorino, 2011: 49–52, figs. 2–4).
- gabbi*, *Macra* – Philippi, 1887a: 145 [1887b: 139], pl. 27, figs. 13, 22. Isla Quiriquina, Hualpen & Tumbez, Chile; Cretaceous. Synonym of *Macra araucana* d'Orbigny, 1842 (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).
- ganae*, *Macra* – Philippi, 1887a: 147–148 [1887b: 141–142], pl. 27, fig. 8; Isla Quiriquina, Chile; Cretaceous. Synonym of *Macra araucana* d'Orbigny, 1842 (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).
- hians*, *Macra* – Philippi, 1846c: 71 [5], pl. 2, fig. 1; 1850o: 138 [12], *non* Pulteney, 1799. Locality unknown. Synonym of the Indian Ocean *Macra rochebrunei* Lamy, 1917, ex Jousseume ms (Lamy, 1917: 214–215).
- hualpensis*, *Macra* – Philippi, 1887a: 146 [1887b: 140], pl. 29, fig. 7. Hualpen, Chile; Cretaceous. Synonym of *Macra araucana* d'Orbigny, 1842 (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).
- ignobilis*, *Macra* – Philippi, 1887a: 153 [1887b: 147], pl. 27, fig. 19. Navidad, Chile; Tertiary [Miocene].
- involuta*, *Macra* “?” – Philippi, 1887a: 149 [1887b: 142], pl. 30, fig. 7a, 7b. Locality unknown, Chile; Francisco J. Ovalle collection; Tertiary.
- jonasi*, *Macra* – Philippi, 1893a: 11–12, pl. 3, fig. 10. Copiapó, Chile. Syntype, MNHNS 229 (n = 1, 68.2 mm x 56.6 mm). Synonym of *Mulinia bicolor* Gray, 1837 (Dall, 1909: 286; Bernard, 1983: 40).
- largillierti*, *Macra* – Philippi, 1849i: 152; 1850o: 135 [9], pl. 3, fig. 1. Gabon, Guinea; Largilliert. Syntypes, NHMUK 1923.7.13.12 (n = 1) (72.4 mm x 53.6 mm) (appears to be figured specimen); Muséum de Rouen 142209041 (n = 1) (80.9 mm x 61.4 mm); MNHNS 188 (n = 1, 78.8 mm x 57.4 mm); SMF 316277 (n = 2) (80.0 mm x 59.4 mm; 73.5 mm x 54.9 mm); SMF 316278 (n = 5 valves) (largest 19.5 mm x 14.6 mm). *Macra largillierti* Philippi, 1849 (Nicklès, 1950: 208, fig. 396; Huber, 2010: 441; 2015: 833–834).
- latis*, *Lutraria elliptica* – Philippi, 1844g: 7. Sicily, Italy. Synonym of the eastern Atlantic *Lutraria lutraria* (Linnaeus, 1758) (Sabelli et al., 1990: 314).
- lebuensis*, *Macra* – Philippi, 1887a: 150 [1887b: 144], pl. 29, fig. 8. Lebu, Chile; Tertiary.



- lenos*, *Mactra* – Philippi, 1887a: 149–150 [1887b: 143–144], pl. 32, fig. 11. Matanzas, Chile; Tertiary.
- lepida*, *Mactra* – Philippi, 1887a: 153 [1887b: 147], pl. 31, fig. 9. Lebu, Chile; Tertiary.
- lotensis*, *Mactra* – Philippi, 1893a: 10–11, pl. 3, fig. 8. Lota, Chile. Holotype, MNHNS 225 (58.7 mm x 45.0 mm) (Signorelli & Pastorino, 2011: figs. 6n–o). Synonym of *Mulinia edulis* (King, 1832) (Dall, 1909: 286; Bernard, 1983: 40), or of *Mulinia byronensis* Gray, 1837 (Signorelli & Pastorino, 2011: 53–55, figs. 6–7).
- lurida*, *Mactra* – Philippi, 1850o: 136, pl. 3, fig. 3. Liew-Kiew [Ryukyu Islands, Japan]; Largilliert. Possible syntype, MNHNS 51645 (not found in March 2014). Synonym of *Mactra cuneata* Gmelin, 1791 (Huber, 2010: 440, 754).
- macilenta*, *Lutraria* – Philippi, 1887a: 164 [1887b: 157–158], pl. 33, fig. 13. Isla Quiriquina, Chile; Cretaceous. Possibly a synonym of *Lutraria cuneiformis* Hupé, 1854 (Wetzel, 1930: 80).
- magellanica*, *Mactra* – Philippi, 1893a: 10, pl. 2, fig. 6. Strait of Magellan, Chile. Syntype, MNHNS 216 (n = 1, 45.9 mm x 35.7 mm). Bernard (1983:55) incorrectly listed this as a synonym of *Eurhomalea exalbida* (Dillwyn, 1817). Güller & Zelaya (2016a: Supplementary Materials, at 7, 11) stated that “the study of the holotype of *Mactra magellanica* reveals its conspecificity with the syntypes of *Mulinia edulis*” (King, 1832).
- martini*, *Lutraria* – Philippi, 1887a: 165 [1887b: 159], pl. 33, fig. 5. Lebu; Tertiary. Syntypes, SGO.PI.374 (n = 1, labeled as “lectotipo”); SGO.PI.4821 (n = 1, labeled as “paralectotipo”). *Mactra (Labiosa) martini* (Philippi, 1887); Miocene (Tavera, 1979: 82, pl. 15, fig. 32).
- medinae*, *Mactra* – Philippi, 1887a: 151 [1887b: 145], pl. 29, fig. 9. Hacienda la Cueva; Tertiary [Pliocene].
- navicula*, *Venus* “?” – Philippi, 1887a: 117 [1887b: 111], pl. 19, fig. 6. Hualpen & Isla Quiriquina, Chile; Cretaceous. Synonym of *Mactra araucana* d’Orbigny, 1842 (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).
- nesaea*, *Mactra* – Philippi, 1887a: 146 [1887b: 140], pl. 32, fig. 12. Isla Quiriquina, Chile; Cretaceous. Synonym of *Mactra araucana* d’Orbigny, 1842 “?” (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).
- nitida*, *Mactra* – Philippi, 1887a: 152 [1887b: 146], pl. 27, fig. 10. Navidad, Chile; Tertiary [Miocene].
- nucleus*, *Mactra* – Philippi, 1887a: 155 [1887b: 149], pl. 32, fig. 3. Cahuil, Chile; Quaternary.
- oblonga*, *Mactra* – Philippi, 1887a: 152 [1887b: 146], pl. 27, fig. 18. Navidad, Chile; Tertiary. *Mactra oblonga* Philippi, 1887; Miocene (Frassinetti & Covacevich, 1994: 85–86, figs. 21, 22).
- olorina*, *Mactra* – Philippi, 1846c: 72 [6], pl. 2, fig. 2. Red Sea. Possible syntype, MNHNS 51614 (not found in March 2014). *Mactra olorina* Philippi, 1846 (Sabelli et al., 1990: 313; Lamprell & Whitehead, 1992: pl. 37, fig. 247; Oliver, 1992: 131, pl. 27; Huber, 2010: 442, 755), recently introduced into the eastern Mediterranean (Streftaris et al., 2005: 449).
- ovallei*, *Mactra* “?” – Philippi, 1887a: 149 [1887b: 142], pl. 29, fig. 6. Locality unknown [Chile]; Francisco J. Ovalle collection; Tertiary.
- oxyrrhyncha*, *Mactra* – Philippi, 1887a: 147 [1887b: 141], pl. 27, fig. 7. Hualpen & Isla Quiriquina, Chile; Cretaceous. Synonym of *Mactra araucana* d’Orbigny, 1842 (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).
- paitensis*, *Mactra* – Philippi, 1893a: 12, pl. 3, fig. 11. Paita, Peru. Syntype, MNHNS 228 (n = 1 valve, 95.7 mm x 73.0 mm). Synonym of *Mulinia velata* Philippi, 1849 (Dall, 1909: 286), or *Mactra (Mactroderma) paitensis* Philippi, 1893 (Bernard, 1983: 39).
- pencana*, *Mactra* – Philippi, 1893a: 8, pl. 1, fig. 2. Talcahuano, Penco, Chile; Tomé. Holotype, MNHNS 224 (63.7 mm x 49.2 mm) (Signorelli & Pastorino, 2011: figs. 6j–k). Synonym of *Mulinia byronensis* Gray, 1837 (Dall, 1909: 286; Signorelli & Pastorino, 2011: 53–55, figs. 6–7).
- plebeja*, *Mactra* – Philippi, 1887a: 153 [1887b: 147], pl. 31, fig. 11. Lebu, Chile; Tertiary.
- ponderosa*, *Mactra* – Philippi, 1844w: 165–166 [1–2], pl. 1, fig. 1, *non* Conrad, 1830, *non* Eichwald, 1830. Western Atlantic. Syntypes, SMF 316281 (n = 3) (“Boston”) (125.6 mm x 88.2 mm; 98.3 mm x 67.8 mm; 62.7 mm x 43.3 mm). Synonym of *Mactromeris polynyma* (Stimpson, 1860) (Bernard, 1983: 40; Kantor & Sysoev, 2005: 393).
- pulchella*, *Mactra* – Philippi, 1846c: 71–72 [5–6], pl. 2, fig. 3. China; Largilliert. Possible syntype, MNHNS 51644 (not found in March 2014). The western Pacific *Mactra pulchella* Philippi, 1846 (Higo et al., 1999: 476; Huber, 2010: 442, 754).
- pulla*, *Mactra* – Philippi, 1849i: 152; 1850o: 137 [11], pl. 3, fig. 4. Gabon, Guinea; Largilliert.



- Syntypes, MNHNS 51643 (n = 2, largest, 18.3 mm x 13.1 mm). Synonym of *Macra sauliana* (Gray, 1838) (Huber, 2015: Excel file on CD). Erroneously listed by Bernard (1983: 53) under *Tivela byronensis* (Gray, 1838) in the Veneridae.
- pusilla*, *Macra* – Philippi, 1887a: 153–154 [1887b: 147], pl. 27, fig. 14. Navidad & Lebu, Chile; Tertiary. *Macra pusilla* Philippi, 1887; Miocene (Frassinetti & Covacevich, 1994: 86, figs. 23–24; Frassinetti, 2001: 78, 2004: 74).
- quiriquinae*, *Macra* – Philippi, 1887a: 145 [1887b: 139], pl. 29, fig. 7. Isla Quiriquina, Chile; Cretaceous. Syntypes, SGO.PI.199 (n = 1, labeled as “lectotipo”); SGO.PI.4731, 4732 (n = 1, each labeled as “paralectotipo”). Synonym of *Macra araucana* d’Orbigny, 1842 “?” (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).
- remondi*, *Macra* – Philippi, 1887a: 150 [1887b: 144], pl. 30, fig. 1. Coquimbo, Chile; Ang. Rémond; Tertiary. Holotype, SGO.PI.204.
- rostrata*, *Macra* – Philippi, 1849i: 152–153; 1849z5: 452; 1850o: 138 [12], pl. 3, fig. 6, *non* Spengler, 1802. Galveston, Texas; Römer. Syntypes, MNHNS 213 (n = 2 valves, larger, 13.2 mm x 11.5 mm; smaller, 13.2 mm x 10.7 mm). Synonym of *Mulinia lateralis* (Say, 1822) (Dall, 1894: 104–105; Lamy, 1918: 339–340).
- sagei*, *Macra* – Philippi, 1887a: 150 [1887b: 144], pl. 31, fig. 1. Corral & Valdivia, Chile; Carlos Sage; Tertiary.
- scolia*, *Macra* – Philippi, 1887a: 148 [1887b: 142], pl. 31, fig. 10. Algarrobo, Chile; Cretaceous.
- senegalensis*, *Macra* – Philippi, 1849s: 27. Senegal; Largilliert. Syntypes, MNHNS 51603 (n = 2 specimens + 1 valve; largest, 30.0 mm x 22.5 mm). Muséum de Rouen 14210632 is from Gabon, not Senegal, hence not type material. Cosel (1995: 52) determined that Philippi’s description was of a juvenile *Macra glabrata* (Linnaeus, 1767), known from Angola and South Africa, and the subsequent citations of this species as “*Standella senegalensis* (Philippi, 1849)” (e.g. Nicklès, 1950: 210, fig. 401) were a distinct taxon, *Raeta senegalica* Cosel, 1995.
- senex*, *Lutraria* – Philippi, 1887a: 165–166 [1887b: 159], pl. 33, fig. 12. Lebu, Chile; Tertiary. Holotype, SGO.PI.375.
- simplex*, *Macra* – Philippi, 1887a: 153 [1887b: 146–147], pl. 27, fig. 9. Navidad; Tertiary [Miocene].
- solida*, *Lutraria* – Philippi, 1851c: 78–79. Mediterranean. Synonym of the eastern Atlantic *Lutraria lutraria* (Linnaeus, 1758) (Huber, 2010: 759).
- spectabilis*, *Lutraria* – Philippi, 1851c: 79. East Indies. *Nomen dubium* (Huber, 2010: 754, 760).
- splendidula*, *Macra* – Philippi, 1887a: 154 [1887b: 147–148], pl. 27, fig. 16. Navidad, Chile; Tertiary [Miocene].
- steinmanni*, *Macra* “?” – Philippi, 1887a: 146 [1887b: 140], pl. 29, fig. 12. Tumbez near San Vicente, Chile; Cretaceous. Synonym of *Macra araucana* d’Orbigny, 1842 (Wilckens, 1904: 251–260, pl. 20, figs. 5–7).
- subangulata*, *Macra* – Philippi, 1887a: 148 [1887b: 142], pl. 29, fig. 1. Algarrobo, Chile; Cretaceous. Holotype, SGO.PI.205 (n = 1 valve). *Macra subangulata* Philippi, 1887 (Fuenzalida, 1953: 138–144, figs. 1–2).
- sulcata*, *Macra* – Philippi, 1887a: 154 [1887b: 148], pl. 27, fig. 20, *non* Reeve, 1854. Navidad, Chile; Tertiary [Miocene].
- tenuis*, *Lutraria* – Philippi, 1845i: 50. Gregory Bay, Strait of Magellan, Chile. Syntypes, ZMB 112740 (40.9 mm x 20.0 mm) (Signorelli & Pastorino, 2011: fig. 14h (as “holotype”, which is not a valid lectotype designation); ZMB 112741 (n = 6 valves) (Signorelli & Pastorino, 2011: figs. 14i–l (as “paratypes”); SMF 316258 (n = 2 non-matching valves) (51.5 mm x 24.0 mm; 48.9 mm x 23.7 mm). Synonym of *Darina solenoides* (King, 1832) (Ihering, 1907: 458; Bernard, 1983: 41; Huber, 2010: 761; Signorelli & Pastorino, 2011: 61–64, figs. 14–16).
- tenuis*, *Macra* – Philippi, 1857: 405–406; 1887a: 152 [1887b: 146], pl. 29, fig. 11, *non* Montagu, 1803 [Abra]. Hacienda de La Cueva [1857] & Matanzas [added in 1887a], Chile; Tertiary. SGO.PI.202, from Matanzas, is the specimen referenced in 1887, but it is not from the original (1857) type locality.
- truncatula*, *Macra* – Philippi, 1887a: 154 [1887b: 148], pl. 27, fig. 15. Navidad, Chile; Tertiary [Miocene].
- undata*, *Lutraria* – Philippi, 1887a: 164 [1887b: 158], pl. 33, figs. 8, 10, 11. Tubul (Volckmann) & Lebu (Kulezewski), Chile; Tertiary. Syntypes, SGO.PI.369 (n = 1, Lebu); SGO.PI.376 (n = 1, Lebu); SGO.PI.4745, 4746 (n = 1, both from Lebu).
- vaga*, *Macra* – Philippi, 1887a: 151 [1887b: 145], “pl. 32, fig. 4” [however, the caption to fig. 4 stated “*Tellina* (non descripta)”. Isla Santa Maria, Chile; Tertiary.
- valdiviana*, *Macra* – Philippi, 1887a: 150 [1887b: 144], pl. 31, fig. 4. Corral, Chile; Carlos Sage; Tertiary.



*varians*, *Mactra* – Philippi, 1887a: 154–155 [1887b: 148–149], pl. 30, fig. 9. Cahuil, Chile; Quaternary.

*velata*, *Mactra* – Philippi, 1849i: 153; 1850o: 137–138 [11–12], pl. 3, fig. 5. Panama; E. B. Philippi. The Panamic *Standella velata* (Philippi, 1849) (Ramírez et al., 2003: 268; Huber, 2010: 444; Coan & Valentich-Scott, 2012: 550–551, pl. 181); type species (OD) of *Mactroderma* Dall, 1894, now regarded as a junior synonym of *Standella* Gray, 1853.

*vetula*, *Lutraria* – Philippi, 1887a: 165 [1887b: 159], pl. 33, fig. 3. Llancahue, Chile; Wilhelm Frick; Tertiary. Syntypes, SGO.PI.370 (n = 1, labeled as “lectotipo”); SGO.PI.4747 (n = 1, labeled as “paralectotipo”).

*vicentina*, *Mactra* – Philippi, 1887a: 148 [1887b: 142], pl. 36, fig. 10. Tumbez Peninsula near San Vicente, Chile; Cretaceous. Synonym of *Mactra araucana* d’Orbigny, 1842 “?” (Wilckens, 1904: 251–260, pl. 20, figs. 5–7), or as *Cymbophora araucana* (d’Orbigny, 1842) (Stinnesbeck, 1986: 176, pl. 4, figs. 10–12, but erroneously citing *Lyonsia vicentina* Philippi, 1887, for this species).

*vidali*, *Mactra* – Philippi, 1887a: 154 [1887b: 148], pl. 30, fig. 6. Mejillones del Sur & Caldera, Chile; Quaternary.

*volckmanni*, *Lutraria* – Philippi, 1887a: 164–165 [1887b: 158], pl. 33, fig. 6. Lota (Volckmann) & Lebu (MacSporran), Chile; Tertiary. Syntypes, SGO.PI.366 (n = 1 valve, from Lota, labeled as “holotipo”); SGO.PI.372 (n = 1 specimen + 1 valve, from Lebu).

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“*Moulinea*” & “*Mulina*” – Philippi, 1853a: 471. Misspellings of *Mulinia* Gray, 1837.

“*Moulinia*” – Philippi, 1844w: 166. A misspelling of *Mulinia* Gray, 1837.

#### Mesodesmatidae

*Donacilla* – Philippi, 1836a: viii, 37, *non* Blainville, 1819 [suppressed]. Type species (OD): *Donacilla lamarckii* Philippi, 1836 (ICZN Opinion 1141, 1979). The ICZN suppressed Blainville’s name (itself a junior synonym of *Amphidesma* Lamarck, 1818), in order to conserve Philippi’s name. Recent, Mediterranean.

*corrugata*, *Donacilla* – Philippi, 1887a: 156 [1887b: 149–150], pl. 23, fig. 13. Lebu, Chile; Tertiary. Holotype, SGO.PI.453.

*lamarckii*, *Donacilla* – Philippi, 1836a: viii, 37–38. “Tyrrheno” [Tyrrhenian Sea, north

coast of Sicily], Mondello, Palermo & Cafalù, Sicily, Italy. Synonym of *Donacilla cornea* (Poli, 1791) (Sabelli et al., 1990: 314; Kantor & Sysoev, 2005: 395, as *D. “lamarcki”*).

#### Ungulinidae

*apicalis*, *Diplodonta* – Philippi, 1836a: viii, 31, pl. 4, fig. 6; 1844g: 24. Palermo & Trepani, Sicily, Italy. Synonym of *Diplodonta trigona* (Scacchi, 1835) (Sabelli et al., 1990: 302, but who listed it as the senior synonym, with Scacchi’s earlier name in synonymy; Aartsen, 2001: 47, 50; Cretella et al., 2005: 126), or as *Microstagon trigona* (Scacchi, 1835) (Huber, 2015: 828).

*dilatata*, *Diplodonta* – Philippi, 1836a: viii, 31, pl. 4, fig. 7. Red Sea. Also fossil: Palermo “calcareo” & Militello “tufo basaltico”. This description was found to be a composite of two species when Philippi subsequently determined that the fossil material from Italy was a junior synonym of *Diplodonta rotundata* (Montagu, 1803) (Philippi, 1844g: 279 [Index]). This was confirmed by Sabelli et al. (1990: 302) and Aartsen (2001: 47). The Recent material from the Red Sea likely represents what is now *D. subrotundata* Issel, 1869 (Oliver, 1992: 102, pl. 21, fig. 2a, b; Huber, 2015: 332, 816), which would be a junior synonym of Philippi’s species.

*inconspicua*, *Diplodonta* – Philippi, 1845i: 53; 1860a: 175 [1860b: 157]. Isla Chiloe, Chile. Syntypes, MNHNS 202 (n = 1, 22.8 mm x 21.9 mm); SMF 315742 (n = 4 valves) (largest, 8.0 mm x 7.3 mm); ZMB 3256 (n = 5 valves) (largest, 20.3 mm x 18.8 mm). The Chilean Pleistocene to Recent *Diplodonta inconspicua* Philippi, 1845 (Dall, 1909: 263; Herm, 1969: 115, pl. 3, figs. 5–7; Valdovinos, 1999: 154; Letelier et al., 2003: 121; Nielsen, 2013: 52, 54, figs. 10e–h; Güller & Zelaya, 2016a: 237), or *Felaniella inconspicua* (Philippi, 1845) (Bernard, 1983: 30; Reid & Osorio, 2000: 134, 136, fig. 4N; Ramírez et al., 2003: 267).

*lunularis*, *Diplodonta* – Philippi, 1844z4: 46, [86], pl. 2, fig. 7. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Lectotype, RPMH (Hildesheim), designated by Janssen (1979b: 96–97); one paralectotype, RPMH. *Grotriana lunularis* (Philippi, 1844) (Glibert & Van de Poel, 1970: 85; Janssen, 1979b: 96–97, pl. 2, fig. 49).

*minuta*, *Diplodonta* – Philippi, 1887a: 184 [1887b: 177], pl. 24, fig. 10. Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.463



( $n = 1$  valve, labeled as “lectotipo”); SGO.PI.4795, 4796 ( $n = 1$  valve each, labeled as “paralectotipo”).

*obliqua*, *Diplodonta* – Philippi, 1846h: 20–21. Mazatlán, Sinaloa, Mexico. *Diplodonta* (*Microstagon*) *obliqua* Philippi, 1846 (Coan & Valentich-Scott, 2012: 744–745, pl. 230), or *Microstagon obliqua* (Philippi, 1846) (Huber, 2015: 828).

*semiaspera*, *Diplodonta* – Philippi, 1836b: 225–226, 235 [pl. expl.], pl. 7, fig. 2. Havana, Cuba. The western Atlantic *Diplodonta semiaspera* Philippi, 1836 (Rios, 1994: 256, pl. 88, fig. 1252; Mikkelsen & Bieler, 2007: 244; Tunnell et al., 2010: 344; Redfern, 2013: 418–419, fig. 1115; Huber, 2015: 338, 825–826; Zelaya, 2016: 255, some using the genus or subgenus *Phlyctiderma*). Type species (OD) of *Phlyctiderma* Dall, 1899.

#### Veneridae

*accepta*, *Venus* – Philippi, 1887a: 132 [1887b: 126], pl. 16, fig. 8. Coquimbo, Chile; Tertiary. Syntypes, SGO.PI.156 ( $n = 1$ , labeled as “lectotipo”); SGO.PI.146 ( $n = 1$ , labeled as “paralectotipo”). Synonym of *Eurhomalea coquimbana* (Philippi, 1887) (Herm, 1969: 127–128, pl. 12, figs. 9–11; Frassinetti, 1974: 44).

*adansonii*, *Cytherea* – Philippi, 1844x: 169 [3], pl. 2, fig. 2. Senegal. Synonym of the eastern Atlantic *Dosinia lupinus* (Linnaeus, 1758) (Fischer-Piette & Delmas, 1967: 17).

*adenensis*, *Cytherea* – Philippi, 1848g: 73 [41], pl. 9, fig. 6. Aden, Red Sea; Th. Philippi. Synonym of *Circentia callipyga* (Born, 1778) (Issel, 1869: 66; Oliver, 1992: 183–184, pl. 41).

*agrestis*, *Venus* – Philippi, 1845i: 54; 1845v: 62 [13], pl. 4, fig. 1. Strait of Magellan, Chile. Syntype, MNHNS 194 (22.4 mm x 24.1 mm). Huber (2010: 710) thought this might be a misplaced specimen of the later-named Californian *Globivenus fordii* (Yates, 1890); more likely a junior synonym of *Ameghinomya antiqua* (King, 1832), from Chile (Bernard, 1983: 51; Pérez et al., 2013: 370–371, figs. 3.1, 3.4, 3.7).

*alfonsoi*, *Venus* – Philippi, 1887a: 132 [1887b: 126], pl. 18, fig. 6. Coquimbo, Chile; Tertiary. Syntypes, SGO.PI.154 ( $n = 1$ , labeled as “lectotipo”); SGO.PI.174 ( $n = 1$ , labeled as “paralectotipo”).

*alta*, *Venus* – Philippi, 1887a: 116 [1887b: 110], pl. 20, fig. 3. Algarrobo, Chile; Ludwig Landbeck; Cretaceous.

*amabilis*, *Venus* – Philippi, 1847r: 90–91; 1848h: 75–76 [23–24], pl. 7, fig. 2. Locality unknown. Possible syntype, MNHNS 239 ( $n = 1$  valve, “Oc. In.” [Indian Ocean], 73.8 mm x 47.7 mm, broken). The western Pacific *Paphia amabilis* (Philippi, 1847) (Abbott & Dance, 1982: 364; Higo et al., 1999: 510; Okutani et al., 2000: 1014–1015, fig. 56; Qi, 2004: 313–314, pl. 170E; Huber, 2010: 421).

*amathusia*, *Venus* – Philippi, 1844m: 129 [7], pl. 2, fig. 4. Locality unknown. The Panamic *Chionopsis amathusia* (Philippi, 1844) (Ramírez et al., 2003: 269; Huber, 2010: 375; Coan & Valentich-Scott, 2012: 763–765, pl. 235). Type species (OD) of *Chionopsis* Olson, 1932.

*amoena*, *Cytherea* – Philippi, 1845i: 53–54. “Pacific Ocean”.

*analís*, *Venus* – Philippi, 1851c: 125–126. Locality unknown.

*angulosa*, *Cytherea* (*Artemis*) – Philippi, 1847p: 229 [31], pl. 6, fig. 1. Malaccas & Philippines. The western Pacific *Dosinella angulosa* (Philippi, 1847) (Higo et al., 1999: 506), or as *Dosinia* (*Dosinella*) *angulosa* (Philippi, 1847) (Fischer-Piette & Delmas, 1967: 70–71; Okutani, 2000: 1010–1011, fig. 42; Huber, 2010: 414). Type species (OD) of *Dosinella* Dall, 1902.

*anus*, *Cytherea* (*Artemis*) – Philippi, 1847w: 23 [35], pl. 8, fig. 1; 1849h: 132–133. Locality unknown (collector given as Gruner in 1849h). The New Zealand *Dosinia* (*Austrodosinia*) *anus* (Philippi, 1847) (Powell, 1979: 423, pl. 77, fig. 1; Abbott & Dance, 1982: 361, both as “1848”; Beu, 2006: 272–274, fig. 31; Huber, 2010: 414); type species (OD) of *Austrodosinia* Dall, 1902.

*apicalis*, *Cytherea* – Philippi, 1836a: viii, 40–41, 42, pl. 4, fig. 5. Palermo, Sicily, Italy. Also fossil. Synonym of *Gouldia minima* (Montagu, 1803) (Sabelli et al., 1990: 327).

*araneosa*, *Venus* – Philippi, 1847r: 91; 1848h: 77 [25], pl. 7, fig. 6. Locality unknown. Possible syntype, MNHNS 244 ( $n = 1$  valve, 45.0 mm x 30.8 mm, but no locality). The Indo-Pacific *Tapes araneosa* (Philippi, 1847) (Huber, 2010: 420, 740–741).

*araucana*, *Venus* – Philippi, 1887a: 123 [1887b: 117], pl. 17, fig. 6. Tubul & Navidad, Chile; Tertiary. Syntypes, SGO.PI.122 ( $n = 1$ , Tubul) (Frassinetti, 1974: 46 listed this as the “holotipo” but this is not a valid lectotype designation under ICZN Code Article 74.6 (1999)); SGO.PI.114 ( $n = 1$  valve, Tubul); SGO.PI.125 ( $n = 1$ , Tubul); SGO.PI.4859–4862



- (all Tubul) (all lots other than 122 labeled as "paralectotipo"). *Eurhomalea araucana* (Philippi, 1887) (Frassinetti, 1974: 47, figs. 1, 2; 1997: 74, 70–71, pl. 2, figs. 9–11; Frassinetti & Covacevich, 1995: 54–55, pl. 1, fig. 18), or a synonym of *Retrotapes exalbidus* (Dillwyn, 1817), Pliocene to Recent (Nielsen & Valdovinos, 2008: 206–207, fig. 12).
- astartoides*, *Venus* – Philippi, 1849o: 61 [35], ex Beck ms. Arctic Ocean. Synonym of *Lio-cyma fluctuosum* (Gould, 1841) (Coan et al., 2000: 386–387); in the latter, it was credited to Middendorff, 1849, ex Beck ms, but Middendorff's work appeared after August 1849, whereas Philippi's appeared in April 1849 and thus takes precedence.
- australis*, *Venus* – Philippi, 1868: 225–226, *non* Gmelin, 1791, *non* G. B. Sowerby I, 1835, *non* Quoy & Gaimard, 1835. Strait of Magellan, Chile; William? Acton.
- birmanica*, *Cytherea* – Philippi, 1848g: 74 [44], pl. 9, fig. 8. Mergui Archipelago, Burma [Myanmar]; Th. Philippi. Synonym of *Sunetta donacina* (Gmelin, 1791).
- boliviana*, *Venus* (*Cytherea*) – Philippi, 1887a: 135 [1887b: 129], pl. 58, fig. 7. Mejillones, Bolivia [now Chile]; Quaternary. The Pliocene *Macrocallista boliviana* (Philippi, 1887) (Herm, 1969: 124, pl. 11, figs. 3, 4; DeVries & Frassinetti, 2003: 125–126; pl. 2, fig. 5).
- bravardi*, *Venus* – Philippi, 1893b: 9–10, pl. 1, fig. 4. Argentina; Tertiary. "*Venus*" *bravardi* Philippi, 1893; Miocene (del Río & Martínez, 1998: 72, pl. 21, fig. 8); *Chione bravardi* (Philippi, 1893) (Ihering, 1907: 386).
- buchanani*, *Venus* – Philippi, 1887a: 127 [1887b: 121], pl. 22, fig. 2. Guayacán, Chile; Tertiary. Syntypes, SGO.PI.158 (*n* = 1 valve, labeled as "lectotipo"); SGO.PI.166 (*n* = 1 valve, labeled as "paralectotipo"). Synonym of *Eurhomalea lenticularis* (G. B. Sowerby I, 1835) (Herm, 1969: 128–129, pl. 13, figs. 1–4; Frassinetti, 1974: 44).
- cahuilensis*, *Venus* – Philippi, 1887a: 135 [1887b: 129], pl. 21, fig. 9. Cahuil, Chile; Quaternary. Syntypes, SGO.PI.148 (*n* = 1 valve, labeled as "lectotipo"); SGO.PI.181 (*n* = 1 valve, labeled as "paralectotipo").
- calcareia*, *Venus* – Philippi, 1844y: 175 [9], pl. 3, fig. 1. Cuba; Largilliert. Synonym of *Merccaria campechiensis* (Gmelin, 1791).
- calophylla*, *Venus* – Philippi, 1836b: 229–230, 235 [pl. expl.], pl. 8, fig. 2. China Sea. Syntypes, SMF 316150 (*n* = 2) (Canton) (32.2 mm x 29.0 mm; 33.5 mm x 28.4 mm). The western Pacific *Clausinella calophylla* (Philippi, 1836) (Abbott & Dance, 1982: 367, as *Bassina*; Lamprell & Whitehead, 1992: pl. 62, fig. 475, as *Placamen*; Higo et al., 1999: 501; Swennen et al., 2001: 92, fig. 180, as *Placamen*; Qi, 2004: 310, pl. 169C, as *Clausinella*; Poppe, 2011: 272–273, pl. 1131, figs. 4–7, as *Placamen*). According to Huber (2010: 369, 715), Philippi's species is more likely a synonym of *Placamen lamellatum* (Röding, 1798). Misspelled by some authors as *V. "callophyla"*.
- caryum*, *Venus* "?" – Philippi, 1887a: 129 [1887b: 123], pl. 21, fig. 4. Lebu, Chile; Francisco J. Ovale; Tertiary.
- chiloensis*, *Venus* – Philippi, 1887a: 121–122 [1887b: 116], pl. 15, fig. 6. Ancud; Strait of Magellan, Chile; Tertiary. Syntypes, SGO.PI.113 (Frassinetti, 1974: 48, fig. 6 listed this as the "holotipo", but this is not a valid lectotype designation under ICZN Code Article 74.6 (1999)); SGO.PI.94, SGO.PI.5104–5109 (Pérez et al., 2013: 369–370). *Chione chiloensis* (Philippi, 1887) (Ihering, 1907: 350; Frassinetti, 1974: 48, fig. 6), or as *Ameghinomya chiloensis* (Philippi, 1887) (Pérez et al., 2013: 369–370, figs. 2.2, 2.7); Miocene (Frassinetti, 2006: 65). *Venus chiloensis sensu* Ortmann (1900: 378) *non* Philippi described as *Chione cossmanni* Ihering, 1907 (Parodiz, 1996: 215).
- chlorotica*, *Venus* – Philippi, 1849q: 186–187; 1849y: 82 [38], pl. 10, fig. 3. China "?". Syntype, MNHNS 233 (*n* = 1, 23.6 mm x 22.6 mm). The Indo-Pacific *Placamen chloroticum* (Philippi, 1849) (Abbott & Dance, 1982: 367, as *Clausinella*; Huber, 2010: 368; Poppe, 2011: 274–275, pl. 1132, fig. 7).
- cicercula*, *Venus* – Philippi, 1887a: 129 [1887b: 123], pl. 21, fig. 10. Navidad, Chile; Tertiary [Miocene]. Syntype, SGO.PI.168 (*n* = 1 valve).
- colchaguensis*, *Venus* – Philippi, 1887a: 122–123 [1887b: 117], pl. 17, fig. 4. La Cueva, Chile; Domeyko; Tertiary [Pliocene]. Holotype, SGO.PI.120. *Eurhomalea colchaguensis* (Philippi, 1887) (Frassinetti, 1974: 46, fig. 3), or as *Retrotapes colchaguensis* (Philippi, 1887) (del Río, 1997: 78), or synonym of *Retrotapes fuenzalidae* (Philippi, 1887) (Nielsen, 2013: 52, figs. 9a–h). Nielsen (2013: 52) noted that Frassinetti (1974) "incorrectly assumed that *V. colchaguensis* has priority because it appears earlier in Philippi's (1887) text. *Venus fuenzalidae* is here selected as the valid name for this species, because it has diagnostic syntypes, while the holotype of *V. colchaguensis* is an internal mold."



- comis*, *Venus* – Philippi, 1887a: 133 [1887b: 127], pl. 16, fig. 3. Coquimbo, Chile; Tertiary. Syntypes, SGO.PI.151 (n = 1, labeled as “lectotipo”); SGO.PI.152 (n = 1) and SGO.PI.4883 (n = 1) (both labeled as “paralectotipo”).
- complanata*, *Artemis* – Philippi, 1887a: 114 [1887b: 108], pl. 15, fig. 1. Matanzas; Tertiary. Syntype, SGO.PI.457 (n = 1 valve, labeled as “lectotipo”, but the original description refers to multiple specimens).
- compressa*, *Venus* – Philippi, 1887a: 120 [1887b: 114], pl. 58, fig. 4, *non* Linnaeus, 1771, *non* Montagu, 1808, *non* Brown, 1833. Isla Quiriquina, Chile; Cretaceous. Holotype, SGO.PI.185 (n = 1). Synonym of *Cytherea auca* (d’Orbigny, 1846) (Wilckens, 1904: 243–248, pl. 19, figs. 2–4), or of *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- contracta*, *Cytherea* (*Arthemis*) – Philippi, 1844x: 172 [6]. East Indies. The western Pacific *Dosinia* (*Asa*) *contracta* (Philippi, 1844) (Fischer-Piette & Delmas, 1967: 36–37, pl. 8, figs. 6, 11; Huber, 2010: 412).
- controversa*, *Venus* – Philippi, 1887a: 132 [1887b: 126], pl. 31, fig. 3 [figure from d’Orbigny]. For *Venus auca* (d’Orbigny 1843) [as *Macra*], *non* *V. auca* d’Orbigny, 1841. Coquimbo, Chile; Hanet Cléry; [Cenozoic]. d’Orbigny described both *Macra auca* d’Orbigny (1843: 125, pl. 14, figs. 19, 20) and *Venus auca* d’Orbigny (1841, pl. 12, figs. 17, 18; 1843: 122). Philippi transferred *Macra auca* to *Venus*, creating a junior secondary homonym that he thought required renaming. D’Orbigny’s type missing; *nomen dubium* (Griffin & Nielsen, 2008: 258). Recent dating of d’Orbigny’s work now allows us to know that his captioned plate 12 appeared in 1841, whereas plate 14 appeared in 1843 along with the text, so the wrong species was renamed.
- coquimbana*, *Venus* – Philippi, 1887a: 125 [1887b: 119], pl. 19, fig. 2. Coquimbo, Chile; Claudio Gay; Tertiary. Holotype, SGO.PI.164 (n = 1 valve). The Pliocene *Eurhomalea coquimbana* (Philippi, 1887) (Herm, 1969: 127–128, pl. 12, figs. 9–11; Frassinetti, 1974: 44).
- crassa*, *Venus* – Philippi, 1887a: 123 [1887b: 117], pl. 21, fig. 1, 1b, 1c, *non* Gmelin, 1791. Hacienda La Cueva, Chile [; Domeyko]; Tertiary [Pliocene]. Syntypes, SGO.PI.87 (n = 1 valve, labeled as “lectotipo”), SGO.PI.138 (n = 1 valve, labeled as “paralectotipo”) (Frassinetti, 1974: 48, fig. 5). Synonym of *Amiantis domeykoana* (Philippi, 1887), Pliocene (Frassinetti, 1974: 48, fig. 5; Nielsen, 2012: 52–53, fig. 10a–d).
- crassula*, *Venus* – Philippi, 1887a: 122 [1887b: 116], pl. 15, figs. 3a, 3b, 4, var. Coquimbo & Isla Mocha, Chile; Tertiary. Syntypes, SGO.PI.129 (n = 1, Coquimbo, labeled as “lectotipo”); SGO.PI.98 (n = 1, Coquimbo, labeled as “paralectotipo”); SGO.PI.121 (n = 1, Isla Mocha); SGO.PI.4858 (n = 1, Coquimbo, labeled as “paralectotipo”). Synonym of *Chionopsis petitiana* (d’Orbigny, 1841) (Herm, 1969: 121–122, pl. 10, figs. 5–10; Frassinetti, 1974: 44; Griffin & Nielsen, 2008: 281, pl. 14, figs. 1, 2).
- darwinii*, *Venus* – Philippi, 1857: 406; 1887a: 122 [1887b: 116], pl. 17, fig. 2. Santa Cruz, Chile; Ramón Vidal Gormáz; Tertiary. Holotype, SGO.PI.97 (Frassinetti, 1974: 48, fig. 7). *Chione darwini* (Philippi, 1887) (Ihering, 1907: 307; Frassinetti, 1974: 48, fig. 7) or as *Ameghinomya darwini* (Philippi, 1887) (Bernard, 1983: 51; Pérez et al., 2013: 366, figs. 2.2, 2.7); Oligocene-Miocene (Frassinetti & Covacevich, 1999: 38–39, pl. 7, fig. 6).
- decipiens*, *Venus* – Philippi, 1841f: 11; 1844z4: 11, [86], pl. 2, fig. 9. Tertiary near Wilhelms Höhe, Hessen, Germany [Late Oligocene]. Type material lost (R. Janssen, pers. comm., April 2013).
- decussata*, *Venerupis* – Philippi, 1836a: vii, 22, pl. 3, fig. 5; 1844g: 20. Palermo, Sicily, Italy & Ionian Sea. Syntypes, SMF 316059 (n = 2) (Panormio) (larger, 11.2 mm x 10.2 mm). Synonym of *Lajonkairia substriata* (Montagu, 1808) (Sabelli et al., 1990: 332) or of *Lajonkairia lajonkairii* (Payraudeau, 1826) (Huber, 2010: 433, 751). *Venerupis decussata* is the type species (SD P. Fischer, 1887) of *Lajonkairia* Deshayes, 1854.
- diazii*, *Venus* – Philippi, 1887a: 119 [1887b: 113], pl. 18, fig. 1. Hualpen, Chile; Cretaceous. Holotype, SGO.PI.116 (n = 1 valve). Synonym of *Cytherea auca* (d’Orbigny, 1841) (Wilckens, 1904: 243–248, pl. 19, figs. 2–4), but now *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- dilatata*, *Cytherea* (*Arthemis*) – Philippi, 1844x: 172 [6]. East Indies. Fischer-Piette & Delmas (1967: 87) were unable to determine the status of this species, which they suggested might be a senior synonym of *Dosinia amphidesmoides* (Reeve, 1850), or a junior synonym of *Dosnia exoleta* (Linnaeus, 1758).



- distans*, *Venus* – Philippi, 1851c: 126, Panama; E. B. Philippi. Possible synonym of *Lirophora mariae* (d'Orbigny, 1846) (Coan & Valentich-Scott, 2012: 781–782, pl. 242), or a *nomen dubium* (Bernard, 1983: 52).
- domeykoana*, *Cytherea* – Philippi, 1857: 406; 1887a: 123 [1887b: 117], pl. 21, fig. 2, 2b, 2c, as *Venus*. Hacienda de La Cueva, Chile; Ignacio Domeyko; Tertiary [Pliocene]. *Amiantis domeykoana* (Philippi, 1887) (Herm, 1969: 124–125, pl. 12, figs. 1–3; Frassinetti, 1974: 48, fig. 5; DeVries & Frassinetti, 2003: 125, pl. 2, fig. 2; Nielsen, 2013: 52–53, fig. 10a–d).
- dunkeri*, *Cytherea* – Philippi, 1844x: 170 [4], pl. 2, fig. 5 [not noted in text]. West Mexico. The Panamic *Dosinia dunkeri* (Philippi, 1844) (Dall, 1909: 157, 265; Fischer-Piette & Delmas, 1967: 68–69; Bernard, 1983: 51; Ramírez et al., 2003: 270; Huber, 2010: 410; Coan & Valentich-Scott, 2012: 825–826, pl. 257).
- effossa*, *Venus* – Philippi, 1836a: viii, 43–44, pl. 3, fig. 20a–c, ex Bivona ms.; 1844g: 34. Palermo & Trepani, Sicily, Italy; deep sea. The eastern Atlantic *Globivenus effossa* (Philippi, 1836) (Sabelli, 1990: 326; Huber, 2010: 361). Type species (M) of *Globivenus* Coen, 1934.
- euglypta*, *Venus* – Philippi, 1847r: 89; 1848h: 76 [24], pl. 7, fig. 3. Locality unknown. Possible syntype, ZMB 104211 (ex Dunker) (48.9 mm x 30.9 mm). The western Pacific *Paphia euglypta* (Philippi, 1847) (Abbott & Dance, 1982: 364; Higo et al., 1999: 510; Qi, 2004: 313, pl. 170B; Huber, 2010: 422).
- eunippe*, *Venus* – Philippi, 1887a: 134 [1887b: 128], pl. 22, fig. 6. Coquimbo, Chile; Gay; Tertiary. Syntypes, SGO.PI.173 (n = 1, labeled as “lectotipo”); SGO.PI.149 (n = 1, labeled as “paralectotipo”). Synonym of *Eurhomalea coquimbana* (Philippi, 1887) (Herm, 1969: 127–128, pl. 12, figs. 9–11; Frassinetti, 1974: 44).
- exarata*, *Venus* – Philippi, 1846n: 109–110 [19–20], pl. 5, fig. 6, *non* Bory de Saint-Vincent, 1827. Red Sea “?” [actually Japan]. New name: *Paphia* (*Paphia*) *philippiana* Huber (2010: 422, 741–742). The western Pacific *Paphia exarata* (Philippi, 1846) (Lamprell & Healey, 1998: 254–255, fig. 772; Higo et al., 1999: 510; Okutani, 2000: 1014–1015, fig. 55; Swennen et al., 2001: 94, fig. 194; Qi, 2004: 313, pl. 170A, as “1847”), all of whom missed the homonymy).
- exasperata*, *Cytherea* (*Artemis*) – Philippi, 1847w: 24 [36], pl. 8, fig. 5. Locality unknown. The western Pacific *Phacosoma exasperata* (Philippi, 1847) (Higo et al., 1999: 508) or as *Dosinia exasperata* (Philippi, 1847) (Lamprell & Whitehead, 1992: pl. 72, fig. 573; Qi, 2004: 303, pl. 165C).
- eximia*, *Venus* – Philippi, 1847r: 90; 1849o: 59–60 [33–34], pl. 9, fig. 1, *non* Forbes, 1846 (fossil, India). East Indies. Possible syntype, MNHNS 243 (n = 1 valve, 68.9 mm x 57.7 mm). Synonym of the Caribbean *Puberella crenata* (Gmelin, 1791) (Huber, 2010: 376, 719), or of the eastern Pacific *Chione* (*Chionopsis*) *crenifera* (G.B. Sowerby I, 1835) (Bernard, 1983: 51).
- expallesens*, *Venus* – Philippi, 1844y: 176 [10], pl. 3, fig. 5; 1845i: 54; 1845-l: 54. Chile. Synonym of *Eurhomalea rufa* (Lamarck, 1818) (Dall, 1909: 292; Bernard, 1983: 65).
- fernandezii*, *Venus* – Philippi, 1887a: 125 [1887b: 119], pl. 16, fig. 7. Pucalan, Colchagua, Chile; Ricardo Fernandez Frias; Tertiary. SGO.PI.77, holotype (1 valve) (Frassinetti, 1974: 48, fig. 5). Synonym of *Amiantis domeykoana* (Philippi, 1887) (Nielsen, 2013: 52–53, fig. 10a–d).
- ferrieri*, *Venus* – Philippi, 1887a: 116 [1887b: 110], pl. 17, fig. 8. Isla Quiriquina, Chile; Cretaceous. Holotype, SGO.PI.147 (n = 1 valve). Synonym of *Cytherea auca* (d'Orbigny, 1841) (Wilckens, 1904: 243–248, pl. 19, figs. 2–4), or now *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- foliacea*, *Venus* – Philippi, 1846n: 107–108 [17–18], pl. 5, fig. 1. Red Sea & Madagascar; Petit. (MNHNS 231 comprises 2 valves, but from Zanzibar, so probably not type material). The Indian Ocean *Placamen foliaceum* (Philippi, 1846) (Oliver, 1992: 192, pl. 38, as *Bassina foliacea*; Huber, 2010: 368, 715).
- foncki*, *Venus* – Philippi, 1887a: 128 [1887b: 122], pl. 19, fig. 4. Lebu, Chile; Tertiary.
- fragilis*, *Cytherea* – Philippi, 1844g: 33, 299, pl. 14, fig. 12a, 12b. Palermo; fossil.
- fuenzalidae*, *Venus* – Philippi, 1887a: 125 [1887b: 119], pl. 19, fig. 3. Hacienda La Cueva, Chile; Tertiary [Pliocene]. *Eurhomalea fuenzalidae* Philippi, 1887) (Herm, 1969: 128, pl. 12, figs. 15, 16, emended to “*fuenzalida*”). Syntypes, SGO.PI.83 (n = 1, labeled as “lectotipo”); SGO.PI.90 (n = 1 valve), SGO.PI.4863–4866, SGO.PI.5092–5094 (all labeled as “paralectotipo”). Synonym of *Eurhomalea colchaguensis* (Philippi, 1887) (Frassinetti, 1974: 46, fig. 3), or a valid species, *Retrotapes fuenzalidae* (Philippi, 1887)



- (DeVries & Frassinetti, 2003: 126, pl. 2, fig. 6; Nielsen, 2013: 52, figs. 9a–h). Nielsen (2013: 52) noted that Frassinetti (1974) “incorrectly assumed that *V. colchaguensis* has priority because it appears earlier in Philippi’s (1887) text. *Venus fuenzalidae* is here selected as the valid name for this species, because it has diagnostic syntypes, while the holotype of *V. colchaguensis* is an internal mold.”
- gigantea*, *Cytherea* (*Arthemis*) – Philippi, 1844x: 171 [5], ex G. B. Sowerby I ms., *non Venus gigantea* Gmelin, 1791 (possible senior secondary homonym). Locality unknown; Anton. *Venus cycloides* d’Orbigny, 1846: 562, *nom. nov. pro Cytherea gigantea* Philippi, *non* Gmelin. Synonym of *Dosinia ponderosa* (Gray, 1838), eastern Pacific (Bernard, 1983: 51; Coan & Valentich-Scott, 2012: 825).
- gilva*, *Venus* – Philippi, 1849q: 187–188; 1849y: 82–83 [38–39], pl. 10, fig. 4. Locality unknown; Largilliert. Type material not found in Muséum de Rouen (Huber, 2015: Chapter 5 on CD). *Placamen gilvum* (Philippi, 1849) (Lamprell & Whitehead, 1992: pl. 62, fig. 474; Huber, 2010: 368).
- gruneri*, *Artemis* – Philippi, 1849h: 132. Locality unknown; Gruner. NHMUK 1923.7.3.11, in type collection (41.1 mm x 42.8 mm), but with note by E. Fischer-Piette (1946), “Ceci n’est pas le type de Philippi, ni l’échantillon figure par Reeve. C’est probablement un *altior* Deshayes”) [This is not Philippi’s type, nor the specimen figured by Reeve, and it is probably *altior* Deshayes]. *Dosinia* (*Austrodosinia*) *gruneri* (Philippi, 1849), from southeast Asia (Fischer-Piette & Delmas, 1967: 54–55, fig. 3).
- gruneri*, *Cytherea* (*Artemis*) – Philippi, 1847w: 23–24 [35–36], pl. 8, fig. 2. Locality unknown. The western Pacific *Phacosoma gruneri* (Philippi, 1847) (Higo et al., 1999: 508) or *Dosinia* (*Asa*) *gruneri* (Philippi, 1844) (Huber, 2010: 412).
- hians*, *Donax* (*Cytherea*) – Philippi, 1851c: 74–75. Locality unknown. Syntype, MNHNS 51854 (n = 1, 53.7 mm x 42.7 mm). Römer (1862) discussed its differences from *Tivela* (*Planitivella*) *planulata* (Broderip & G. B. Sowerby I, 1830). Synonym of the Panamic *Tivela* (*Planitivella*) *lessonii* (Deshayes, 1830) (Bernard, 1983: 53; Coan & Valentich-Scott, 2012: 832–834, pl. 259).
- hualpensis*, *Venus* – Philippi, 1887a: 120 [1887b: 114], pl. 21, fig. 6. Hualpen, Chile; Cretaceous. Pl. 19, fig. 7 is also labeled “*V. hualpensis*”, but it is something different than the cited figure. Synonym of *Cytherea auca* (d’Orbigny, 1841) (Wilckens, 1904: 243–248, pl. 19, figs. 2–4), but now of *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- hupeana*, *Venus* – Philippi, 1887a: 132–133 [1887b: 126–127], pl. 26, fig. 1. Coquimbo, Chile; Tertiary. Holotype, SGO.PI.186 (n = 1). Synonym of *Eurhomalea hanetiana* (d’Orbigny, 1841), Pliocene (Herm, 1969: 127, pl. 12, figs. 12–14; Frassinetti, 1974: 44).
- hyalina*, *Venus* – Philippi, 1849y: 83–84 [39–40], pl. 10, fig. 6. Locality unknown; Largilliert. Synonym of the Australian *Clementia papyracea* (Gray, 1825) (Lamprell & Whitehead, 1992: pl. 73, fig. 580).
- ignobilis*, *Venus* – Philippi, 1844y: 176 [10], pl. 3, fig. 4 [*non* Philippi, 1846z]. Chile. Synonym of *Leukoma thaca* (Molina, 1782) (Dall, 1909: 292; Bernard, 1983: 52, as *Protothaca*).
- ignobilis*, *Venus* – Philippi, 1846z: 152 [22], pl. 6, fig. 2, ex Anton ms, *non* Philippi, 1844y. Locality unknown. Sherborn (1927: 3114) credited the name to “Anton in Philippi”, but Philippi signed the description and the header indicated “in lit.”, so this is interpreted as an Anton ms name. Oddly, he had used the same combination two years before for a completely different species. Synonym of the southeast Asian *Marcia hiantina* (Lamarck, 1818) (Huber, 2015: Chapter 5 on CD).
- incompta*, *Venus* – Philippi, 1836a: viii, 44–45, 48, pl. 4, fig. 9. Catania, Sicily, & Cumano, Naples, Italy. Also fossil. Synonym of *Mysia undata* (Pennant, 1777) (Sabelli et al., 1990: 332).
- indecora*, *Cytherea* – Philippi, 1848g: 74 [44], pl. 9, fig. 7. Mergui Archipelago, Burma [Myanmar]; Th. Philippi.
- ione*, *Venus* – Philippi, 1887a: 118 [1887b: 112], pl. 35, fig. 6a, 6b. East coast of Tumbez Peninsula near San Vicente, Chile; Cretaceous. Syntypes, SGO.PI.182 (n = 1 valve, labeled as “lectotipo”); SGO.PI.4852 (n = 1, labeled as “paralectotipo”). *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- isabillnia*, *Venus* – Philippi, 1849q: 188; 1849y: 83 [39], pl. 10, fig. 5. China. Spelling of species name is demonstrably a double typographic error, in that the species was described as being “... subtriangulari, isabelina, lamellis ...” and was corrected in Philippi (1849y) (ICZN Code Article 32.5 (1999)).



- Ruhoff (1980: 328) listed this species as being by "Philippi, in Reeve" (i.e., Reeve, 1863b: pl. 23, fig. 112), but it was described by Philippi in 1849. The southwestern Pacific *Placamen isabellina* (Philippi, 1849) (Abbott & Dance, 1982: 367, as *Clausinella*; Higo et al., 1999: 501; Swennen et al., 2001: 92, fig. 181; Qi, 2004: 310, pl. 169A; Huber, 2010: 368).
- kochii*, *Venus* – Philippi, 1843e: 41 [3], pl. 1, fig. 4. Locality unknown. Syntype, MNHNS 230 (n = 1 valve, 30.0 mm x 20.8 mm; label gives locality as "Africa"). Synonym of the South African *Eumarcia paupercula* (Holten, 1802).
- kroeyeri*, *Venus* (*Artemis*?) – Philippi, 1847r: 87; 1848h: 78 [26], pl. 7, fig. 9, as *V. kröyeri*. Chile, Peru; Kröyer. Synonym of the Panamic *Cyclinella subquadrata* (Hanley, 1844) (Coan & Valentich-Scott, 2012: 823–824, pl. 256). Erroneously treated as a synonym of the New Zealand *Dosinia lambata* (Gould, 1846) by some authors (Fischer-Piette & Delmas, 1967: 29). Type material not located; type locality clarified as being Paita, Piura, Peru (Coan, 2001: 352).
- laeviuscula*, *Artemis* "?" – Philippi, 1887a: 115 [1887b: 109], pl. 19, fig. 1. Santa Cruz, Patagonia, Chile; Tertiary. Syntype, SGO.PI.4715 (n = 2 valves). *Dosinia laeviuscula* (Philippi, 1887) (Ihering, 1907: 301, 348; Frassinetti, 1975: 219, fig. 7). Frassinetti (1975: 219) cited SGO.PI.189 as the "holotipo" and SGO.PI.177 as "paratipos" but neither lot was found in March 2014.
- lamelligera*, *Venus* – Philippi, 1887a: 126–127 [1887b: 121], pl. 14, fig. 6. Matanzas, Chile; Tertiary. Syntypes, SGO.PI.99 (n = 1 valve, labeled as "lectotipo"); SGO.PI.92 (n = 2 valves, labeled as "paralectotipo"); SGO.PI.5096 (n = 6 valves, labeled as "paralectotipo"). Synonym of *Venus navidadis* Philippi, 1887 (Frassinetti, 1974: 47; later transferred to *Retrotapes*).
- landbecki*, *Venus* – Philippi, 1887a: 116 [1887b: 110], pl. 20, fig. 8. Algarrobo, Chile; Ludwig Landbeck; Cretaceous. Syntype, SGO.PI.157 (n = 1 valve); this lot is on a single block that also has the type material of *Tellina landbecki* Philippi, 1887.
- largillierti*, *Venus* – Philippi, 1847r: 87–88; 1849o: 60–61 [34–35], pl. 9, fig. 3. New Zealand; Largilliert. Figured syntype, MNHNS 238 (53.9 mm x 40.1 mm). *Venerupis* (*Paphirus*) *largillierti* (Philippi, 1847) (Powell, 1979: 426, pl. 77, fig. 14; Abbott & Dance, 1982: 365; Lamprell & Healey, 1998: 254–255, fig. 773; Huber, 2010: 427). Type species (OD) of *Paphirus* Finlay, 1926.
- lens*, *Venus* – Philippi, 1841f: 11; 1844z4: 11, [86], pl. 2, fig. 10. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. Perhaps synonym of *Pelecypora suborbicularis* (Goldfuss, 1841) (Rust, 1999: 52–53; R. Janssen, pers. comm., April 2013). Type material lost (R. Janssen, pers. comm., April 2013).
- lepida*, *Venus* – Philippi, 1887a: 129–130 [1887b: 123–124], pl. 22, fig. 8. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.153 (n = 1 valve).
- lirata*, *Venus* – Philippi, 1848h: 76–77 [24–25], pl. 7, fig. 5 [*non* Philippi, 1887a/b]. Locality unknown. The western Pacific *Paphia lirata* (Philippi, 1848) (Higo et al., 1999: 510; Qi, 2004: 313, pl. 170H; Huber, 2010: 422, 741).
- lirata*, *Venus* "?" – Philippi, 1887a: 126 [1887b: 120], pl. 21, fig. 8, *non* Philippi, 1848h. Lebu; Tertiary. Syntypes, SGO.PI.89 (n = 1 valve, labeled as "lectotipo"); SGO.PI.5110 (n = 1 valve, labeled as "paralectotipo").
- livida*, *Cytherea* – Philippi, 1845i: 54. "Pacific Ocean". Synonym of *Megapitaria aurantiaca* (G. B. Sowerby I, 1831) (Huber, 2010: 407, 733).
- livida*, *Cytherea* (*Artemis*) – Philippi, 1847p: 230 [32], pl. 6, fig. 4, *non* Philippi, 1845. Locality unknown. Either a preoccupied *nomen dubium* species of *Dosinia* (M. Huber, in litt., 7 Jan. 2014), or a junior synonym of *Dosinia lupinus* (Linnaeus, 1758) (Fischer-Piette & Delmas, 1967: 17).
- macsporrani*, *Venus* – Philippi, 1887a: 123–124 [1887b: 118], pl. 21, fig. 7, as "*V. Mac-Sporran*". Lebu; MacSporran; Tertiary. Holotype, SGO.PI.84 (n = 1).
- mactraeformis*, *Venus* – Philippi, 1887a: 124 [1887b: 118], pl. 20, fig. 1. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.96 (n = 1 valve).
- maxima*, *Venus* – Philippi, 1846z: 151–152 [21–22], pl. 6, fig. 1, ex Anton ms. Locality unknown. Sherborn (1928: 3926) credited the name to "Anton in Philippi", but Philippi signed the description and the header indicated "in lit.", so this is interpreted as an Anton ms name. Synonym of *Saxidomus gigantea* (Deshayes, 1839), northeastern Pacific (Coan et al., 2000: 384).
- mendanae*, *Cytherea* – Philippi, 1851b: 72. Marquesas; Bernardi. Synonym of the Indo-Pacific *Lioconcha* (*Sulcilioconcha*) *philippinarum* (Hanley, 1844) (Higo et al., 1999: 505).



- modesta*, *Cytherea* – Philippi, 1845d: 198 [20], pl. 3, fig. 3, *non* G. B. Sowerby I, 1835. Philippine Islands. Homonym renamed as *Dione philippii* Deshayes, 1853. Synonym of *Pitar inflatus* (G. B. Sowerby II, 1851) (Huber, 2010: Chapter 5 on CD).
- navidadis*, *Venus* – Philippi, 1887a: 126 [1887b: 120–121], pl. 14, fig. 4. Navidad, Chile; Tertiary. Holotype, SGO.PI.134 (Frassinetti, 1974: 47, fig. 4). *Venus* (*Marcia*) *navidadis* Philippi, 1887; Miocene (Feruglio, 1937: 178; Tavera, 1979: 80, pl. 13, figs. 20–21), or *Retrotapes navidadis* (Philippi, 1887) (del Río, 1997: 78; Frassinetti, 2006: 65, fig. 6).
- neomeris*, *Venus* – Philippi, 1887a: 118 [1887b: 112], pl. 30, fig. 10. East coast of Tumbez Peninsula near San Vicente, Chile; Cretaceous. Syntypes, SGO.PI.136 (*n* = 1, labeled as “lectotipo”); SGO.PI.4853 (*n* = 1 valve, labeled as “paralectotipo”). Synonym of *Cytherea auca* (d’Orbigny, 1846) (Wilckens, 1904: 243–248, pl. 19, figs. 2–4), or now *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- nephele*, *Venus* – Philippi, 1887a: 117 [1887b: 111], pl. 18, fig. 4. Hualpen, Chile; Cretaceous. Synonym of *Cytherea auca* (d’Orbigny, 1846) (Wilckens, 1904: 243–248, pl. 19, figs. 2–4), or now of *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- nitens*, *Venus* – Scacchi & Philippi, in Philippi, 1844g: 35–36, 299, pl. 14, fig. 14a–c, *non* Turton, 1819. Naples, Italy. Synonym of *Paphia* (*Politapes*) *lucens* (Locard, 1886) (Sabelli et al., 1990: 330), or of *Paphia aurea* (Gmelin, 1791) (Cretella et al., 2005: 128).
- nucula*, *Cytherea* – Philippi, 1849h: 144. Peru or Chile; Kröyer. *Tivela* (*Planitivela*) *nucula* (Philippi, 1849), from Peru (Bernard, 1983: 53; Ramírez et al., 2003: 269).
- nuculiformis*, *Venus* – Philippi, 1887a: 120 [1887b: 114], pl. 58, fig. 3. Hualpen, Chile; Cretaceous. Syntypes, SGO.PI.192 (*n* = 1, labeled as “lectotipo”); SGO.PI.4855, 4856 (*n* = 1 valve each, labeled as “paralectotipo”). *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- oblonga*, *Cytherea* (*Venus*) – Philippi, 1893b: 10, pl. 1, fig. 1. Argentina; Tertiary. *Tivela* (*Pachydesma*) *oblonga* (Philippi, 1893); Miocene (del Río, 1991: 65–66, pl. 5, figs. 1–3; del Río & Martínez, 1998: 73, pl. 20, figs. 1–2).
- oenoe*, *Venus* – Philippi, 1887a: 134–135 [1887b: 128–129], pl. 58, fig. 14. Guayacán, Chile; Tertiary. Syntypes, SGO.PI.190 (*n* = 1, labeled as “lectotipo”); SGO.PI.142 (*n* = 1 valve, labeled as “paralectotipo”). Synonym of *Eurhomalea coquimbana* (Philippi, 1887) (Herm, 1969: 127–128, pl. 12, figs. 9–11; Frassinetti, 1974: 45).
- ovallei*, *Venus* – Philippi, 1887a: 124 [1887b: 118], pl. 20, fig. 7. Lebu, Chile; Francisco J. Ovalle; Tertiary.
- pacheia*, *Venus* – Philippi, 1893b: 10, pl. 1, fig. 2. Argentina; Tertiary. Possibly a junior synonym of *Chionopsis munsterii* (d’Orbigny, 1839), Miocene (del Río, 1991: 69–70, pl. 4, fig. 6; del Río & Martínez, 1998: 77, pl. 14, figs. 8–9, pl. 20, figs. 5–6, pl. 26, figs. 2–3; Griffin & Nielsen, 2008: 275–276, pl. 8, figs. 5, 6).
- patagonica*, *Cytherea* – Philippi, 1844x: 169 [3], pl. 2, fig. 1. “Patagonia; Largilliert” [actually Caribbean]. Synonym of *Dosinia concentrica* (Born, 1778) (Fischer-Piette & Delmas, 1967: 63, 65). Philippi’s species was unnecessarily renamed *Venus philippii* d’Orbigny, 1846, on the grounds that it was given a geographically inappropriate name.
- patagonica*, *Venus* – Philippi, 1887a: 121 [1887b: 114], pl. 17, fig. 3. Santa Cruz, Patagonia, Chile; Tertiary. Holotype, SGO.PI.127 (Frassinetti, 1974: 49, fig. 9). *Chione patagonica* (Philippi, 1887); Miocene (Ihering, 1907: 309; Frassinetti, 2001: 77, 2004: 74, 2006: 65–66, fig. 7); Oligocene-Miocene (Frassinetti & Covacevich, 1999: 40, pl. 7, figs. 9, 10).
- pencana*, *Venus* – Philippi, 1887a: 119 [1887b: 113], pl. 20, fig. 2. Hualpen, Chile; Cretaceous. Synonym of *Cytherea auca* (d’Orbigny, 1841) (Wilckens, 1904: 243–248, pl. 19, figs. 2–4), but now regarded as a synonym of *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- pfeifferi*, *Cytherea* – Philippi, 1847r: 86; 1848g: 71–72 [39–40], pl. 9, fig. 1. Locality unknown. Issel (1869: 66) cited Philippi’s description and figure and recorded this species from the Red Sea, but erroneously gave the species name as *Circe* “*liturata*” [sic; *litturata*], which was described by Gray in 1838. It seems subsequently to have disappeared from the literature, including that for the Red Sea.
- punguis*, *Venus* – Philippi, 1887a: 131 [1887b: 125], pl. 16, fig. 5. Coquimbo, Chile; Tertiary. Holotype, SGO.PI.150 (*n* = 1). Synonym



- of *Chionopsis petitiana* (d'Orbigny, 1841) (Herm, 1969: 121–122, pl. 10, figs. 5–10; Frassinetti, 1974: 45; Griffin & Nielsen, 2008: 281, pl. 14, figs. 1, 2).
- placida*, *Venus* – Philippi, 1844m: 128 [6], pl. 2, fig. 2. Tasmania, Australia. The South Australian *Placamen placidum* (Philippi, 1844) (Lamprell & Whitehead, 1992: pl. 62, fig. 469; Huber, 2010: 368). Type species (OD) of *Placamen* Iredale, 1925.
- plagia*, *Venus* – Philippi, 1887a: 133 [1887b: 127], pl. 18, fig. 5. Coquimbo, Chile; Tertiary. Syntypes, SGO.PI.187 (n = 1, labeled as “lectotipo”); SGO.PI.194 (n = 1, labeled as “paralectotipo”).
- polita*, *Venus* – Philippi, 1887a: 126 [1887b: 120], pl. 15, fig. 8, *non* Röding, 1798. Araucanerland, Chile; Tertiary. Holotype, SGO.PI.93 (n = 1).
- polydora*, *Venus* – Philippi, 1887a: 134 [1887b: 128], pl. 15, fig. 7. Coquimbo, Chile; Tertiary. Holotype, SGO.PI.184 (n = 1; label indicates this may be a synonym of *Eurhomalea coquimbana* (Philippi, 1887)).
- profundata*, *Venus* – Philippi, 1887a: 124 [1887b: 118], pl. 20, fig. 4. Lebu, Chile; Francisco J. Ovalle; Tertiary.
- promaucana*, *Venus* – Philippi, 1887a: 122 [1887b: 116], pl. 14, fig. 7. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.78 (n = 1).
- pubescens*, *Cytherea* (*Artemis*) – Philippi, 1847w: 24 [36], pl. 8, fig. 3. Locality unknown. Probable syntypes, NHMUK 1840.4.5.47–48 (4 valves) (“Madagascar”). The western Pacific *Pardosinia pubescens* (Philippi, 1847) (Higo et al., 1999: 508); previously listed as a junior synonym of *Dosinia tumida* (Gray, 1838) (Fischer-Piette & Delmas, 1967: 37, 39).
- pucalanensis*, *Venus* – Philippi, 1887a: 125 [1887b: 119–120], pl. 16, fig. 2. Pucalan, Colchagua, Chile; Ricardo Fernandez Frias; Tertiary. Syntype, SGO.PI.100 (n = 1 valve).
- puella*, *Cytherea* – Philippi, 1844g: 33, pl. 14, 299, fig. 13a–c. Northern Italy; fossil. The Pliocene *Callista puella* (Philippi, 1844) (Glibert & Van de Poel, 1966b: 66).
- pulla*, *Cytherea* – Philippi, 1851b: 73. Locality unknown. Synonym of the Panamic *Tivela byronensis* (Gray, 1838) (Dall, 1909: 284; Coan & Valentich-Scott, 2012: 829–830, pl. 258).
- quiriquinae*, *Artemis* – Philippi, 1887a: 113 [1887b: 107], pl. 13, fig. 21. Isla Quiriquina, Chile; Cretaceous. Holotype, SGO.PI.710 (n = 1 valve) (Frassinetti, 1975: 219–220, fig. 2).
- Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- remondi*, *Venus* – Philippi, 1887a: 124 [1887b: 118–119], pl. 15, fig. 9. Guayacán, Chile; Buchanan; Tertiary. Holotype, SGO.PI.155 (n = 1). Synonym of *Chionopsis petitiana* (d'Orbigny, 1841) (Herm, 1969: 121–122, pl. 10, figs. 5–10; Frassinetti, 1974: 45; Griffin & Nielsen, 2008: 281, pl. 14, figs. 1, 2).
- rimosa*, *Venus* – Philippi, 1847r: 88; 1848h: 77 [25], pl. 7, fig. 7. Locality unknown. Syntype, MNHNS 195 (n = 1, 51.7 mm x 31.0 mm, from “China”). Synonym of the western Pacific *Paphia undulata* (Born, 1778) (Lamprell & Whitehead, 1992: pl. 76, fig. 605; Higo et al., 1999: 510).
- rodriguezi*, *Venus* – Philippi, 1887a: 125–126 [1887b: 120], pl. 20, fig. 6. Near Punta Arenas, Strait of Magellan, Chile; Lorenzo Rodriguez; Tertiary. Holotype, SGO.PI.80 (n = 1 valve). *Macrocallista rodriguezi* (Philippi, 1887) (Ihering, 1907: 349), or *Protothaca thaca* (Molina, 1782) (Bernard, 1983: 52).
- rubicunda*, *Cytherea* (*Artemis*) – Philippi, 1847p: 230 [32], pl. 6, fig. 5. Red Sea. Synonym of *Dosinia* (*Dosinella*) *hepatica* (Lamarck, 1819) (Fischer-Piette & Delmas, 1967: 82–84).
- rubiginosa*, *Cytherea* – Philippi, 1845d: 197–198 [19–20], pl. 3, fig. 2. Locality unknown. Synonym of the western Atlantic *Pitar fulminatus* (Menke, 1828).
- rustica*, *Venus* – Philippi, 1887a: 118–119 [1887b: 113], pl. 19, fig. 8. Hualpen, Chile; Cretaceous. Synonym of *Cytherea auca* (d'Orbigny, 1841) (Wilckens, 1904: 243–248, pl. 19, figs. 2–4), but now recognized as a separate species, *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- saginata*, *Venus* – Philippi, 1887a: 134 [1887b: 128], pl. 22, fig. 3. Coquimbo, Chile; Tertiary. Holotype, SGO.PI.188 (n = 1).
- sao*, *Venus* – Philippi, 1887a: 134 [1887b: 128], pl. 18, fig. 3, pl. 26, fig. 2, “var.”. Coquimbo, Chile; Claudio Gay; Tertiary. Syntype, SGO.PI.193 (n = 1, labeled as “lectotipo”).
- scabra*, *Artemis* – Philippi, 1849r: 19. Liewkiew Island [Ryukyu Islands, Japan]; Largilliert. Synonym of the western Pacific *Dosinia histrio* (Gmelin, 1791) (Fischer-Piette & Delmas, 1967: 52; Higo et al., 1999: 509).
- scabriuscula*, *Cytherea* (*Artemis*) – Philippi, 1847p: 229–230 [31–32], pl. 6, fig. 2. Loanda. The Indian Ocean *Dosinia* (*Asa*) *scabriuscula*



- (Philippi, 1844) (Kantor & Sysoev, 2005: 388; Huber, 2010: 412); previously listed as a synonym of *Phacosoma tumida* (Gray, 1838) by Fischer-Piette & Delmas (1967: 37), Higo et al. (1999: 507), and other authors.
- scalenia*, *Venus* – Philippi, 1887a: 120 [1887b: 114], pl. 58, fig. 2. Hualpen, Chile; Cretaceous. Holotype, SGO.PI.180 (n = 1 valve). Synonym of *Cytherea auca* (d'Orbigny, 1841) (Wilckens, 1904: 243–248, pl. 19, figs. 2–4; Wetzel, 1930: 78), or now of *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- scita*, *Venus* – Philippi, 1887a: 129 [1887b: 123], pl. 21, fig. 3. Navidad, Chile; Tertiary [Miocene].
- scolia*, *Venus* – Philippi, 1887a: 133 [1887b: 127–128], pl. 18, fig. 8. Coquimbo, Chile; Tertiary. Holotype, SGO.PI.140 (n = 1). Synonym of *Eurhomalea coquimbana* (Philippi, 1887) (Herm, 1969: 127–128, pl. 12, figs. 9–11; Frassinetti, 1974: 45).
- semilaevis*, *Artemis* – Philippi, 1887a: 113–114 [1887b: 108], pl. 13, fig. 22. Navidad & Curau-ma, Chile; Tertiary. Syntypes, SGO.PI.706 (n = 1 valve), SGO.PI.708 (n = 1 valve); SGO.PI.4714 (n = 1 valve) (all from Navidad). Frassinetti (1975: 220, fig. 1) stated that SGO.PI.706 was the “holotype” and SGO.PI.708 was “paratipos” but not designated as such by Philippi. *Dosinia* (D.) *semilaevis* (Philippi, 1887); Miocene (Frassinetti & Covacevich, 1994: 88–89, figs. 31, 32).
- semirugata*, *Venus* – Philippi, 1847r: 88; 1848h: 76 [24], pl. 7, fig. 4. Locality unknown; Dunker collection. Syntype, ZMB 117925 (51.7 mm x 33.6 mm). The Indo-Pacific *Paphia semirugata* (Philippi, 1847) (Lamprell & Whitehead, 1992: pl. 76, fig. 606; Higo et al., 2001: 190; Swennen et al., 2001: 95, fig. 196; Huber, 2010: 423, 742; Poppe, 2011: 296–297, pl. 1143, figs. 3, 4).
- serva*, *Venus* – Philippi, 1887a: 133 [1887b: 127], pl. 16, fig. 1. Coquimbo, Chile; Tertiary. Holotype, SGO.PI.165 (n = 1). Synonym of *Chionopsis petitiana* (d'Orbigny, 1841) (Herm, 1969: 121–122, pl. 10, figs. 5–10; Frassinetti, 1974: 45; Griffin & Nielsen, 2008: 281, pl. 14, figs. 1, 2).
- solidissima*, *Cytherea* – Philippi, 1851b: 74. California. Synonym of the northeastern Pacific *Tivela stultorum* (Mawe, 1823) (Coan et al., 2000: 379–380, pl. 78).
- spretta*, *Venus* – Philippi, 1887a: 133 [1887b: 127], pl. 16, fig. 6. Coquimbo, Chile; Tertiary. Syntypes, SGO.PI.161 (n = 1, labeled as “lectotipo”); SGO.PI.179 (n = 1, labeled as “paralectotipo”); SGO.PI.4884 (n = 1, labeled as “paralectotipo”). Synonym of *Chionopsis petitiana* (d'Orbigny, 1841) (Herm, 1969: 121–122, pl. 10, figs. 5–10; Frassinetti, 1974: 45; Griffin & Nielsen, 2008: 281, pl. 14, figs. 1, 2).
- steinmanni*, *Venus* – Philippi, 1887a: 119–120 [1887b: 113–114], pl. 58, fig. 1. Hualpen, Chile; Cretaceous. Syntypes, SGO.PI.137 (n = 1, labeled as “lectotipo”); SGO.PI.4854 (n = 1 valve, labeled as “paralectotipo”). Synonym of *Cytherea auca* (d'Orbigny, 1841) (Wilckens, 1904: 243–248, pl. 19, figs. 2–4; Wetzel, 1930: 78), now *Aphrodina quiriquinae* (Philippi, 1887), Maastrichtian (Stinnesbeck, 1987: 181–183, pl. 3, figs. 8–9).
- subsulcata*, *Venus* – Philippi, 1887a: 115 [1887b: 109–110], pl. 17, fig. 7. Algarrobo; Ludwig Landbeck; Cretaceous. Holotype, SGO.PI.183 (n = 1 valve).
- sulcosa*, *Venus* – Philippi, 1847r: 89; 1848h: 75 [23], pl. 7, fig. 1. Locality unknown. Possible syntype, MNHNS 234 (n = 1 valve, 66.5 mm x 43.9 mm, from “Australia”). The east African *Paphia sulcosa* (Philippi, 1847) (Huber, 2010: 423, 742–743), in which case MNHNS 234 either is not type material or is mislocalized.
- sulphurea*, *Venus deshayesi* – Philippi, 1848h: 77–78 [25–26], pl. 7, fig. 8. Nicobar Islands “?”; Red Sea “?”. Synonym of the Indo-Pacific *Tapes literatus* (Linnaeus, 1758) (Lamprell & Whitehead, 1992: pl. 73, fig. 581).
- tahitensis*, *Cytherea* – Philippi, 1851b: 73. Tahiti. The Polynesian *Pitar tahitensis* (Philippi, 1851) (Huber, 2010: 400).
- tellinaeformis*, *Venus/Cytherea* – Philippi, 1847r: 86–87; 1849o: 59 [33], pl. 9, fig. 1. Locality unknown. Synonym of the west African *Costellipitar cor* (Hanley, 1844) (Huber, 2010: 397, 730).
- tucapelina*, *Venus* “?” – Philippi, 1887a: 130 [1887b: 124], pl. 21, fig. 5a–c. Tucapel near Lebu, Chile; Tertiary. Syntypes, SGO.PI.144 (n = 1 valve, labeled as “lectotipo”); SGO.PI.145 (n = 1 valve, labeled as “paralectotipo”); SGO.PI.5111 (n = 1 valve, labeled as “paralectotipo”).
- uncinata*, *Venus* – Philippi, 1887a: 130 [1887b: 124], pl. 18, fig. 9. “Chiloé”, Chile; Tertiary. Holotype, SGO.PI.191 (n = 1 valve).
- variabilis*, *Venus* – Philippi, 1844y: 178 [12], pl. 3, figs. 8, 9, ex “Mus. Caes. Vindob.” ms. Bombay, India. Synonym of *Marcia marmorata* (Lamarck, 1818) (Higo et al., 1999: 510).



*vicentina, Artemis* – Philippi, 1887a: 113 [1887b: 107], pl. 37, fig. 11. San Vicente, west coast of Tumbes, Chile; Cretaceous. Holotype, SGO.PI.709 (n = 1 valve). *Dosinia vicentina* (Philippi, 1887) (Wilckens, 1904: 242–243), or as *Cyclinella vicentina* (Philippi, 1887) (Frassinetti, 1975: 221–222, fig. 4).

*volckmanni, Venus* – Philippi, 1887a: 121 [1887b: 115], pl. 14, fig. 9. Navidad, Tubul, Millanejo & Lebu, Chile; Tertiary. Syntypes, SGO.PI.141 (Frassinetti, 1974: 49, fig. 10 listed this as the “holotipo”, but this is not a valid lectotype designation under ICZN Code Article 74.6 (1999); Pérez et al., 2013: 369 stated that this was the “lectotype”, but this is not a valid lectotype designation under ICZN Code Article 74.7 (1999)); SGO.PI.91 (n = 1, Millanejo); SGO.PI.119 (n = 1 valve, Navidad); SGO.PI.128 (n = 1 specimen + 2 valves, Navidad); SGO.PI.124 (n = 1 specimen, Lebu); SGO.PI.5086 (n = 1, Lebu) (all labeled as “paralectotipo”). *Chione volckmanni* (Philippi, 1887), or as *Ameghinomya volckmanni* (Philippi, 1887) (Pérez et al., 2013: 369, figs. 2.10, 2.11); Miocene (Frassinetti, 2001: 77–78, 2004: 75, 2006: 65).

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*“africana, Dione”* – Reeve, 1863a: pl. 12, fig. 57, ex Philippi ms. This species was indicated by Ruhoff (1980: 128) as being by “Philippi, in Reeve,” but it was only based on a ms. name in the Cuming collection.

*“discrepans, Venus”* – Pérez et al. (2013: 370–371, figs. 3.1, 3.4, 3.7) cited this as a Philippi name from 1845, and Bernard (1983: 52) as a Philippi name from 1853, but it was first described by G. B. Sowerby, 1835.

*“excisa, Cytherea”* – Philippi, 1844x: 170 [4], pl. 2, fig. 4, ex Chemnitz ms. This was quoted in Sherborn (1926: 2266) as being by Philippi, but Röding (1798) made this name available based on the same Chemnitz figures, and even earlier Gmelin (1791) used the same figures to establish *Venus sinuata*.

*“fulminata, Cytherea”* – Reeve, 1864: pl. 9, fig. 40. This species was indicated by Reeve as being described by Philippi, but it was first described by Menke (1828).

*“juvenilis, Cytherea (Arthemis)”* – Philippi, 1844x: 172 [6]. Sherborn (1927: 3303) credited this name, which was based on Chemnitz figures (Chemnitz, 1782: pl. 38, figs. 405, 407), to Philippi, but Gmelin (1791: 3287) had already proposed *Venus juvenilis* based on fig. 405, as well as *Venus histrio* based on fig. 407.

*“lutea, Cytherea”* – Dall (1909: 284) credited this name to Philippi, but it was described by Koch in Philippi (1845).

*“magellanica, Venus”* – Letelier et al. (2003: 126) credited this name, from Chile, to Philippi, but it was described by Houttuyn (1787: 130), in a work suppressed by the ICZN (Opinion 380, 1956: 8), and was not validated or described by Philippi.

*“ponderosa, Cytherea”* – Philippi, 1844s: 149 [1], pl. 1, fig. 1. This species was listed by Abbott & Dance (1982: 355) as being by Philippi, but the description was signed by Koch (with an added note by Philippi).

*“rostratus, Cytherea”* – Philippi, 1844s: 150 [2], pl. 1, fig. 4. This Brazilian species, now placed in *Pitar*, was listed by Bernard (1983: 54) and Zelaya (2016: 255) as being by Philippi (and incorrectly by Bernard as from the eastern Pacific), but the description was signed by Koch.

*“semicancellata, Venus”* – Philippi, 1843d: 40 [2], pl. 1, figs. 2, 3. Listed by Higo et al. (1999: 511) and by Okutani (2000: 1014–1015, fig. 61) as a Philippi species, it is credited by Philippi to close collaborator Koch. Although lacking a footer signature, several similar descriptions nearby were signed by Koch, so we also credit him with this one as well.

#### Petricolidae

*chiloensis, Petricola* – Philippi, 1845i: 53. Isla Chiloe, Chile. Synonym of *Petricola dactylus* G. B. Sowerby I, 1823 (Coan, 1997: 313).

*costata, Petricola* – Philippi, 1849i: 163. Locality unknown.

*rhyssodes, Petricola* – Philippi, 1887a: 160 [1887b: 154], pl. 25, fig. 12. Locality not indicated, Chile; Quaternary. Synonym of *Petricola rugosa* G. B. Sowerby I, 1834 (Bernard, 1983: 57).

*robusta, Petricola* – Philippi, 1849i: 163. Panama; in *Margaritifera*; E. B. Philippi. Synonym of *Choristodon robustus* (G. B. Sowerby I, 1834) (Coan & Valentich-Scott, 2012: 842–843, 847, pl. 264).

#### Myidae

*tenuis, Mya* – Philippi, 1887a: 163 [1887b: 157], pl. 23, fig. 11, *non* Schroeter, 1802. Coquimbo, Chile; Quaternary. Synonym of *Cryptomya californica* (Conrad, 1837) (Herm, 1969: 129–130, pl. 13, fig. 8; Bernard, 1983: 58).



## Corbulidae

- aequivalvis*, *Corbula* – Philippi, 1836b: 227–228, 235 [pl. expl.], pl. 7, fig. 4. Havana, Cuba. The western Atlantic *Juliacorbula aequivalvis* (Philippi, 1836) (Mikkelsen & Bieler, 2007: 386; Huber, 2010: 469).
- alba*, *Corbula* – Philippi, 1846h: 19. Mazatlán, Sinaloa, Mexico. Synonym of *Corbula nasuta* (G. B. Sowerby I, 1833) (Coan, 2002: 53–57; Coan & Valentich-Scott, 2012: 873–874).
- birostris*, *Corbula* “?” – Philippi, 1887a: 163 [1887b: 156–157], pl. 28, fig. 9a–d. Lota, Chile; Volckmann; Tertiary.
- carinata*, *Corbula* – Philippi, 1841f: 7; 1844z4: 7, [86], pl. 2, fig. 5, *non* Dujardin, 1837. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. Synonym of *Corbula* (*Caryocorbula*) *rugulosa* Koenen, 1884 (Janssen, 1979b: 133–136, who dated Philippi’s species from 1843). Type material lost (R. Janssen, pers. comm., April 2013).
- operculata*, *Corbula* – Philippi, 1848a: 13. St. Thomas, Virgin Islands, 15–18 fms.; Gruner. Synonym of the western Atlantic *Varicorbula limatula* (Conrad, 1846) (Mikkelsen & Bieler, 2007: 382; Tunnell et al., 2010: 384), or as *Vokesula limatula* (Conrad, 1846) (Hallan et al., 2013: 281). Abbott (1958: 137) and Huber (2010: 770; 2015: 839) considered Philippi’s species separable but neither illustrated it.
- paradoxa*, *Corbula* – Philippi, 1845z: 448 [*nomen nudum*]; 1847-l: 45–46, pl. 7, fig. 4a–c. Magdeburg area, Germany; Tertiary; Sack’s collection. *Corbula henckeliusiana* Nyst, 1836, Oligocene of northern Europe (Koenen, 1894a: 1302–1304, pl. 91, figs. 1–6).
- pulchella*, *Corbula* – Philippi, 1893b: 8, pl. 1, fig. 7. Argentina; Tertiary. *Caryocorbula pulchella* (Philippi, 1893), late Miocene (del Río, 1991: 76–77, pl. 1, fig. 7; del Río & Martínez, 1998: 79, pl. 12, figs. 10–11, pl. 14, figs. 11, 19, pl. 21, figs. 9–10; Martínez & del Río, 2002: 183). Reported as living in the southwestern Atlantic; *Corbula* (*Anisocorbula*) *pulchella* Philippi, 1893 (Huber, 2010: 466, 769).

## Pholadidae

- antipodum*, *Pholas* – Philippi, 1847r: 71–72; 1849m: 52 [2], pl. 1, fig. 3. New Zealand; Largilliert. Syntype, MNHNS 187 (n = 1 valve, 50.8 mm x 18.3 mm). Synonym of *Barnea similis* (Gray, 1835) (Powell, 1979: 429, pl. 78, fig. 13, but without this synonymy; Beu, 2006: 295–299).

- birmanica*, *Pholas* – Philippi, 1849m: 51 [1], pl. 1, fig. 1. Mergui Archipelago, Burma [Myanmar]; Th. Philippi. Possible syntype, MNHNS 51761 (not found in March 2014). *Barnea birmanica* (Philippi, 1849) (Huber, 2010: 473, 772).
- macrostoma*, *Pholas* – Philippi, 1858b: 23. Islas Chonos, Chile; Fr. Fonk. Synonym of *Netastoma darwinii* (G. B. Sowerby II, 1849) (Coan & Valentich-Scott, 2012: 892).
- manilensis*, *Pholas* – Philippi, 1847r: 72; 1849m: 51–52 [1–2], pl. 1, fig. 2. Manila, Philippine Islands; Gruner. Figured syntype, MNHNS 186 (n = 1 valve, 53.0 mm x 18.6 mm); Possible syntype, ZMB 117923 (Manila, Gruner; Dunker coll.) (56.8 mm x 18.6 mm). *Barnea manilensis* (Philippi, 1847) (Higo et al., 1999: 518; Okutani, 2000: 1026–1027, fig. 2; Swennen et al., 2001: 99, fig. 222; Qi, 2004: 321, pl. 175C; Kantor & Sysoev, 2005: 395; Huber, 2010: 474, 772–773; Haga, 2011: 392–393, pl. 1191, figs. 4, 5).
- patagonica*, *Pholas* – Philippi, 1887a: 171 [1887b: 164], pl. 42, fig. 8. Santa Cruz, Chile; Ramón Vidal Gormáz; Tertiary. *Pholadidea patagonica* (Philippi, 1887); Oligocene-Miocene (Frassinetti & Covacevich, 1999: 42, pl. 8, fig. 7; Hryniewicz & Gaździcki, 2016).
- remondi*, *Pholas* – Philippi, 1887a: 170–171 [1887b: 164], not figured. Between Coquimbo & Pan de Azucar, Chile; Rémond; Tertiary.
- vibonensis*, *Pholas* – Philippi, 1844g: 4, 299, pl. 13, fig. 5. Monteleone [Vibo Valentia], Sicily, Italy; fossil. Synonym of *Pholadidea loscombiana* Turton, 1819 (Huber, 2010: Excel file on CD).

## Teredinidae

- chilensis*, *Teredina* “?” – Philippi, 1887a: 172 [1887b: 165], pl. 42, fig. 6. Hualpen, Chile; Cretaceous. Syntypes, SGO.PI.641 (multiple specimens). *Teredo chilensis* (Philippi, 1887) (Wilckens, 1904: 264–265; Moll, 1941: 24), although Wetzel (1930: 80–81) thought that Philippi’s species was similar (“ähnlich”) to *T. simplex* Deshayes, 1860 (Eocene of Europe), while Wilckens’ material might be referable to *T. rugaardensis* Grönwall & Harder, 1907 (Paleocene of Europe). Turner (1966: 93) noted that “On the basis of the description and figure it is impossible to tell to which genus [*Teredo* or *Teredina* (Pholadidae)] it really belongs.”
- diazii*, *Teredo* “?” – Philippi, 1887a: 171 [1887b: 165], pl. 51, fig. 10. Holzes, Chiloé, Chile; Wenceslao; Tertiary. Holotype, SGO.PI.639



(n = 1 tube). *Teredo diazi* Philippi, 1887 (Moll, 1941: 27); Turner (1966: 98) noted, "Name based on tubes only."

*gregaria*, *Teredo* – Philippi, 1887a: 171 [1887b: 165], pl. 42, fig. 7. Navidad, Matanzas & Ancud, Chile; Tertiary. Syntypes, SGO. Pl.642 (Ancud, numerous tubes); SGO. Pl.644 (Ancud, numerous tubes). Moll (1941: 31) noted that this was not the same as "*T. gregaria* Blainville, 1820", but Blainville's usage of "*gregaria*" was actually an error for *Teredo gregata* (Lamarck, 1801) (Turner, 1966: 103), so that Philippi's name is not a junior synonym.

*hoffmanni*, *Teredina* – Philippi, 1846r: 44, pl. 7, fig. 2; Osterweddingen, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene. *Jouannetia hoffmanni* (Philippi, 1846) (Koenen, 1894a: 1336–1338, pl. 95, fig. 5; Moll, 1941: 32), although Turner (1966: 104) noted: "Name based on valve only. Is probably a *Teredina* (Pholadidae), though it has been included in the Teredinidae".

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"*palmulata*, *Teredo*" – Philippi, 1836a: vii, 2, pl. 1, fig. 8a, 8b. Although some authors have treated this as a homonymous Philippi species, he referred to *Teredo palmulata* Lamarck, as figured by Delle Chiaie (1829: 28–29, pl. 54, figs. 18, 22, 23, as "*T. bipalmulata*"). Lamarck's (1818) *Teredo palmulata* was an unjustified emendation of his own *Teredo bipalmulata* Lamarck, 1801, which is now regarded as a valid species of *Bankia*. *Xylotrya philippii* Gray, 1851, was proposed for Philippi's and Delle Chiaie's misidentification of Lamarck's *palmulata*, and would thus be a new species based on Philippi (1836a) and Delle Chiaie (1829); it is now regarded as a synonym of *Bankia carinata* (Gray, 1827) (Turner, 1966: 115).

#### Hiatellidae

*antarctica*, *Saxicava* – Philippi, 1845i: 51–52. Isla Chonos, Chile; E. B. Philippi. *Hiatella antarctica* (Philippi, 1845) (Powell, 1951: 79; Bernard, 1983: 59; Valdovinos, 1999: 158; Letelier et al., 2003: 128), or a synonym of *Hiatella arctica* (Linnaeus, 1767) (Huber, 2015: Chapter 5 on CD).

*bivonae*, *Panopaea* – Philippi, 1836a: vii, 8, pl. 2, fig. 1a–c; 1844g: 6. Sicily, Italy. Possible syntypes, PHB MB M.\_\_\_\_ (Z) 33 (n = 6) (missing in 2013). Synonym of *Panomys*

*norvegica* (Spengler, 1793) (Sabelli et al., 1990: 334; Coan et al., 2000: 488; Kantor & Sysoev, 2005: 345).

*buchanani*, *Panopaea* – Philippi, 1887a: 166–167 [1887b: 160], pl. 35, fig. 2. Guayacán, Chile; Tertiary. Syntype, SGO.Pl.255 (n = 1, labeled as "lectotipo" but the original description refers to multiple specimens). Synonym of the Plio-Pleistocene *Panopea oblonga* Philippi, 1887 (Herm, 1969: 130–131, pl. 13, fig. 7).

*chiloensis*, *Panopaea* – Philippi, 1897: 367–368, pl. 5. Punta del Roble, Isla Chiloé, Chile. Syntypes, SGO.Pl.252 (n = 1, labeled as "lectotipo"); SGO.Pl.257 (n = 1, labeled as "paralectotipo"). The Pliocene *Panopea chiloensis* Philippi, 1897 (Frassinetti, 1997: 74–75, 70–71, pl. 2, figs. 12, 13).

*conchotrypa*, *Saxicava* – Philippi, 1845i: 52. In the [New Zealand] *Haliotis iris* Gmelin, 1791. Presumably a *Hiatella*, the global species of which are poorly understood, with *Hiatella arctica* (Linnaeus, 1767) being reported world-wide, including in New Zealand (Powell, 1979: 428, pl. 75, fig. 17).

*corrugata*, *Panopaea* "?" – Philippi, 1847-l: 57, pl. 10a, fig. 13. Magdeburg area, Germany; Tertiary; Sack's collection. Koenen (1894a: 1316–1317, pl. 93, fig. 4) stated that Philippi's species (Oligocene of Germany) was a homonym of *Panopaea corrugata* J. Sowerby, 1850, and he renamed Philippi's species as *Panopaea woodwardi* Koenen, 1894. However, because Philippi's 1847 species predates Sowerby's name by three years, it was Sowerby's species – *Panopea corrugata* J. De C. Sowerby in Dixon, 1850, Eocene of Sussex, England – that required renaming, not Philippi's. Further study of the English Paleogene species is needed to determine the status of Sowerby's species and its relation to *Panopea affinis* (J. Sowerby, 1812) (J. Todd, in litt., 2 Oct. 2014 & 3 Feb. 2016).

*guayacanensis*, *Panopaea* – Philippi, 1887a: 167 [1887b: 161], pl. 34, fig. 2. Guayacán, Chile; Volckmann; Tertiary. Holotype, SGO. Pl.247 (n = 1 valve). Synonym of the Pliocene *Panopea coquimbensis* (d'Orbigny, 1843) (Herm, 1969: 130, pl. 13, figs. 5, 6; Griffin & Nielsen, 2008: 264, pl. 4, fig. 1; Signorelli & Alfaya, 2014: 289, fig. 40); Bernard (1983: 59, 70) incorrectly synonymized this with the western Atlantic *P. abbreviata* (Valenciennes, 1839).

*ibari*, *Panopaea* – Philippi, 1887a: 167 [1887b: 161], pl. 35, fig. 4. Magallanes & Skyring



Water, Chile; Enrique Ibar; Tertiary. Syntype, SGO.PI.246 (n = 1, labeled as “holotipo” but the original description refers to more than one specimen). *Panopaea ibari* Philippi, 1887 (Ihering, 1907: 352).

*macrodon*, *Saxicava* – Philippi, 1851c: 95. Formosa; Cécile via Largilliert. Perhaps a synonym of the presumably widespread *Hiatella arctica* (Linnaeus, 1767) (Huber, 2015: Chapter 5 on CD).

*oblonga*, *Panopaea* – Philippi, 1887a: 167 [1887b: 160], pl. 35, fig. 1. Guayacán, Chile; Tertiary. Syntypes, SGO.PI.250 (n = 1, labeled as “lectotipo”); SGO.PI.4748 (n = 1 valve, labeled as “paralectotipo”). The Plio-Pleistocene *Panopea oblonga* Philippi, 1887 (Herm, 1969: 130–131, pl. 13, fig. 7).

*torresi*, *Panopaea* – Philippi, 1887a: 168 [1887b: 161], pl. 35, fig. 5. Magallanes; Diego Torres, Chile; Tertiary. Holotype, SGO.PI.254 (n = 1). Griffin (1991: 138) stated that the type locality was probably “Tertiary beds exposed in Riesco Island or Skyring Water in southern Chile.” *Panopaea torresi* Philippi, 1887 (Ihering, 1907: 351).

*truncata*, *Saxicava* – Philippi, 1898b: 89. Fiordo Almirantazgo, Strait of Magellan, Chile; C. E. Porter, 1895.

*vetula*, *Panopaea* – Philippi, 1887a: 167 [1887b: 161], pl. 35, fig. 3. Lota, Chile; Volckmann; Tertiary. Holotype, SGO.PI.251 (n = 1).

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“*arctica*, *Saxicava*” – Philippi, 1836a: vii, 20. As “*mihi*” on p. 20, but only for a transfer of *Mya arctica* “Gm.” [Linnaeus, 1758], to *Saxicava*.

#### Solenidae

*abbreviatus*, *Solen* – Philippi, 1843k: 35 [1], pl. 1, fig. 1. Indian Ocean. Synonym of the Indo-Pacific *Solen vagina* Linnaeus, 1758 (Huber, 2015: Chapter 5 on CD).

*albus*, *Solen* – Philippi, 1849i: 174, ex Martyn ms. Locality not stated.

*beckii*, *Solen* – Philippi, 1847z2: 43 [5], pl. 2, fig. 1. Locality unknown. *Nomen dubium* (Huber, 2010: 664).

*elytron*, *Solen* – Philippi, 1887a: 169 [1887b: 162], pl. 34, figs. 10, 11. Algarrobo, Hualpen & Navidad, Chile; Cretaceous. Syntypes, SGO.PI.354 (n = 1 valve, Algarrobo, labeled as “holotipo?”); SGO.PI.355 (n = 1 valve, Hualpen); SGO.PI.361 (n = 1 valve, Algar-

robo); SGO.PI.364 (n = 1 valve, Navidad). *Solena (Eosolen) elytron* (Philippi, 1887) (Griffin, 1991: 135).

*gracilis*, *Solen* – Philippi, 1847r: 72, non J. De C. Sowerby, 1844. Philippine Islands; Gruner. Replacement name: *Solen xishana* Bernard, Cai & Morton, 1993. The western Pacific *Solen xishana* Bernard, Cai & Morton, 1993 (Qi, 2004: 275, pl. 151D, as “*gracilis*”), who had missed the homonymy and new name, but there remains question as to whether Chinese material matches Philippi’s material from the Philippines (Huber, 2010: 665).

*minor*, *Solen ensis* var. – Philippi, 1841f: 6; 1844z4: 44. Wilhelmshöhe, near Cassel [Oligocene]. Synonym of *Solen hausmanni* Schlotheim in Goldfuss, 1841 (Speyer, 1866: 31), now *Ensis hausmanni* (Goldfuss, 1841) (Rust, 1999: 48).

*pictus*, *Solen* – Philippi, 1849i: 174–175, non Chenu, 1843. Locality unknown.

*tenuis*, *Solen* – Philippi, 1836a: vii, 6, pl. 1, fig. 2; 1844g: 5, non W. Wood, 1828, non Broderip & G. B. Sowerby I, 1829, non Gray in Griffith & Pidgeon, 1833 [non Philippi, 1887a]. Sicily, Italy (fossil). Possible syntype, PHB MB M.544 (VI) 55 (n = 1) (missing in 2013). Cosel (1993: 283–286, pl. 10 [cited in text as 1], figs. 36–38, figs. 130–135, 137) mentioned the “holotype”, which he stated was in “ZMB Berlin,” evidently the fossil syntype in the Berlin paleontological collection (and not a specimen in the Recent mollusc collection). Synonym of *Phaxas pellucidus* (Pennant, 1777) (Sabelli et al., 1990: 316), or of *Phaxas (Phaxas) adriaticus* Coen, 1933 (Cosel, 1993; *P. adriaticus* is now a full species restricted to the Mediterranean; R. von Cosel, pers. comm. 2 Sept. 2014).

*tenuis*, *Solen* – Philippi, 1887a: 169–170 [1887b: 163], pl. 34, fig. 7, non W. Wood, 1828, non Broderip & G. B. Sowerby I, 1829, non Gray in Griffith & Pidgeon, 1833, non Philippi, 1836. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.357 (n = 1 valve).

*valdivianus*, *Solen* – Philippi, 1887a: 170 [1887b: 163], pl. 34, fig. 6. Corral, Chile; Carlos Sage; Tertiary. Syntype, SGO.PI.356 (n = 1, labeled as “holotipo” but the original description refers to multiple specimens).

*versicolor*, *Solen* – Philippi, 1847z2: 43–44 [5–6], pl. 2, fig. 3. Locality unknown. Synonym of the Indo-Pacific *Solen sloanii* Gray, 1843 (Higo et al., 1999: 481). Type not located (Cosel, 1990: 299).



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"*tehuelcha, Solen*" – Stuardo (1970: 231), in discussing the species of Solenidae recognized from southern South America, believed that Philippi's citation of *Solen tehuelcha* d'Orbigny (Philippi, 1847z2: 44, pl. 2, fig. 4) might not be conspecific with *Solen thuelcha* Hanley, 1842, and concluded, "If ... Hanley's sample(s) turns out to be a different species, *S. tehuelcha* must be attributed to Philippi and the specimen deposited at the Museo Nacional de Historia Natural, Santiago de Chile, should be selected as the lectotype." However, there is no indication that d'Orbigny and Hanley were referring to different taxa, since Hanley was the first to describe this species (as "*thuelcha*") before d'Orbigny described the same species (as "*tehuelcha*"); Coan & Kabat (2012: 323), discussed Hanley's species.

#### Gastrochaenidae

*heyseana, Gastrochaena* – Philippi, 1847-l: 57, pl. 10a, fig. 9a, b. Röhre. Magdeburg area, Germany; Tertiary. Perhaps *Teredina heyseana* (Philippi, 1847) (R. Janssen, pers. comm., April 2013), or as *Fistulina heyseana* (Philippi, 1847) (Koenen, 1894a: 1329–1331, pl. 95, fig. 10), Oligocene of northern Germany. Note that *Teredina* is in the Teredinidae, whereas *Fistulina* (now *Eufistulana* Eames, 1951) is in the Gastrochaenidae.

*polii, Gastrochaena* – Philippi, 1844g: 3–4; 1845k: 186, as "*G. poliana*". For *G. cuneiformis sensu* Philippi (1836a: 2–3) *non* Spengler, 1783. Sicily, Italy; also fossil. Synonym of *Rocellaria dubia* (Pennant, 1777) (Priolo, 1973b: 67–70; Sabelli et al., 1990: 333; Kantor & Sysoev, 2005: 396).

#### Clavagellidae

*angulata, Clavagella* "?" – Philippi, 1844g: 2–3, 299, as "*C. angulatae*", pl. 13, fig. 3; 1844n: 100. Palermo, Sicily, Italy. Synonym of *Clavagella aperta* G. B. Sowerby, 1823 (Sabelli et al., 1990: 339), or of *C. melitensis* Broderip, 1834 (Priolo, 1973b: 115–116).

*balanorum, Clavagella* – Philippi, 1840b: 181–182, pl. 3, figs. 1–6; 1844g: 1–2, 299, pl. 13, fig. 2; 1844n: 100, ex Scacchi ms. Naples, Italy. Although sometimes credited to Scacchi (1841) (a paper sometimes erroneously dated to 1839), this species first appeared before the end of 1840 in Philippi's

article (Cretella et al., 2005: 128–129, who attributed the name to "Scacchi in Philippi"). Synonym of *Bryopa aperta* (G. B. Sowerby I, 1823) (Huber, 2010: 484, 776).

*goldfussii, Clavagella* – Philippi, 1845z: 448 [*nomen nudum*]; 1846r: 44, pl. 7, fig. 1, made available as *C. goldfussii*; Osterweddingen, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene. *Stirpulina goldfussii* (Philippi, 1846), Early Oligocene (Smith, 1962: 170; Stallwood, 1995: 88).

*maniculatum, Aspergillum* – Philippi, 1836a: vii, 1, pl. 1, fig. 3; 1844g: 1; 1844n: 100. Palermo, Sicily, Italy; fossil [Pliocene]. Synonym of *Stirpulina bacillum bacillaris* (Deshayes, 1830) (Smith, 1962: 170; Stallwood, 1995: 88) or of *Bryopa aperta* G. B. Sowerby I, 1823 (Huber, 2010: 1836).

#### Lyonsiidae

*Entodesma* – Philippi, 1845i: 52–53. Type species (M): *Entodesma chilensis* Philippi, 1845. Recent, Chile.

*aequivalvis, Pandora* "?" – Philippi, 1836a: vii, 18, pl. 1, fig. 11a–c; 1844g: 16, as *P. "aequiv-atris"*. Palermo, Sicily, Italy; fossil "calcareo". "Not a *Pandora*" (Boss, 1965: 416); synonym of *Lyonsia norwegica* (Gmelin, 1791) (Gray, 1840: 306–307).

*chilensis, Entodesma* – Philippi, 1845i: 53; 1847z6: 66, pl. 3, fig. 10. Chiloe, Chile. Synonym of *Entodesma cuneata* (Gray, 1828) (Dall, 1909: 284), or a valid species (Bernard, 1983: 63; Valdovinos, 1999: 158; Letelier et al., 2003: 129); more study is required (Cárdenas et al., 2008: 233).

*vicentina, Lyonsia* – Philippi, 1887a: 162 [1887b: 156], pl. 56, fig. 4. Tumbez Peninsula near San Vicente, Chile; Cretaceous. Holotype, SGO.PI.625 (n = 1 valve). Possibly a synonym of *Monopleura ambigua* Philippi, 1887 (Wilckens, 1904: 226–227, pl. 19, figs. 1–2); if this synonymy is accepted, then this species would be referable to the Nuculanidae. Stinnesbeck (1986: 176) erroneously listed this species, instead of *Mactra vicentina* Philippi, 1887, in the synonymy of *Cymbophora araucana* (d'Orbigny, 1842) (Mactridae).

#### Pholadomyidae

*landbecki, Pholadomya* – Philippi, 1887a: 168 [1887b: 162], pl. 36, fig. 1. Algarrobo, Chile; Ludwig Landbeck; Cretaceous.



*obesa*, *Pholadomya* – Philippi, 1887a: 168 [1887b: 162], pl. 37, fig. 1. Algarrobo, Chile; Ludwig Landbeck; Cretaceous.

*weissii*, *Pholadomya* – Philippi, 1847-I: 45, pl. 7, fig. 3a, b. Magdeburg area, Germany; Tertiary; Oberbergamtes collection. *Pholadomya weissii* Philippi, 1847 (Koenen, 1894a: 1324–1326, pl. 94, figs. 1, 3; R. Janssen, pers. comm., April 2013).

#### Thraciidae

*compressum*, *Galeomma* “?” – Philippi, 1844g: 19, 299, pl. 14, fig. 5. Sicily, Italy. Possible senior synonym of *Galeomma politum* Deshayes, 1855 (Sabelli et al., 1990: 303), but more likely a *nomen dubium* in the Thraciidae (Aartsen, 1996: 52).

*fabula*, *Thracia* – Philippi, 1844g: 17, 299, pl. 14, fig. 3. Puteolis [Pozzuoli], Italy. Synonym of *Thracia distorta* (Montagu, 1803) (Sabelli et al., 1990: 338).

*ovalis*, *Thracia* – Philippi, 1840a: 67; 1844g: 17, 299, pl. 14, fig. 2, non Brown, 1827. Naples, Italy. Palazzi (2002) concluded that this was probably a synonym of *Thracia distorta* (Montagu, 1803), rather than of *Thracia corbuloides* Deshayes, 1830, as had been suggested by Sabelli et al. (1990: 338).

*ventricosa*, *Thracia* – Philippi, 1844g: 17; 1836a: pl. 1, fig. 10a–c. Palermo, Sicily, Italy; fossil. Possible syntypes, PHB MB M.535 (Z) 65 (n = 2) (missing in 2013). His 1836 figure was labeled as *Thracia pubescens* (Pulteney, 1799). Synonym of *Thracia convexa* (W. Wood, 1815) (Sabelli et al., 1990: 338).

#### Laternulidae

*elegans*, *Anatina* – Philippi, 1844z: 161. China; Largilliert. Syntypes, Muséum de Rouen 142107026 (61.5 mm x 27.8 mm); Museum Rouen 142107045 (broken); SMF 315563 (1 specimen + 1 valve) (larger 76.6 mm x 34.7 mm); SMF 315564 (n = 4 valves) (largest 59.0 mm x 27.2 mm); possible syntype NHMUK 197529 (from Hanley collection, with label “*elegans* Philippi from Philippi”). Synonym of *Laternula rostrata* (G. B. Sowerby II, 1839) (Huber, 2010: 495, 782).

#### Periplomatidae

*anguliferum*, *Periploma* – Philippi, 1847r: 73–74; 1849z5: 452. Galveston, Texas. Syntype, ZMB 117924 (Texas; Dunker/Römer) (n = 4

valves); possible syntype, NHMUK 1968359 (n = 3) (Cuming coll.) (largest, 17.4 mm x 10.9 mm). Synonym of *Periploma margaritaceum* (Lamarck, 1801) (Mikkelsen & Bieler, 2007: 196), or more likely of *Periploma inaequale* (C. B. Adams, 1842) (Huber, 2010: 496, 783).

*araucana*, *Anatina* – Philippi, 1887a: 161 [1887b: 155], pl. 23, fig. 14. Lebu, Chile; Tertiary. Holotype, SGO.PI.383. Griffin (1991: 141), after reviewing the type material, stated that Philippi’s *A. araucana*, *A. davilae* and *A. suborbicularis* were all the same species of *Periploma* (*Aelga*), but did not indicate which name was to be used.

*davilae*, *Anatina* – Philippi, 1887a: 161 [1887b: 155], pl. 33, fig. 1. Lebu, Chile; Tertiary. Holotype, SGO.PI.385. Griffin (1991: 141), after reviewing the type material, stated that Philippi’s *A. araucana*, *A. davilae* and *A. suborbicularis* were all the same species of *Periploma* (*Aelga*), but did not indicate which name was to be used.

*oblonga*, *Anatina* – Philippi, 1836a: vii, 8, pl. 1, fig. 4; 1844g: 7; 1844z3: [1, 4]. Sicily, Italy. Synonym of *Cochlodesma praetenue* (Pulteney, 1799) (Sabelli et al., 1990: 339); type species (M) *Calcaraea* Récluz, 1868, a synonym of *Cochlodesma* Couthouy, 1839.

*pusilla*, *Anatina* “?” – Philippi, 1836a: vii, 9, pl. 2, fig. 5; 1844g: 7. Sicily, Italy; fossil “calcareo”.

*suborbicularis*, *Anatina* – Philippi, 1887a: 160 [1887b: 154], pl. 33, fig. 2. Millanejo; Volckmann; Tertiary. Syntypes, SGO.PI.384 (n = 1, labeled as “lectotipo”); SGO.PI.4743, 4744 (n = 1 each labeled as “paralectotipo”). Griffin (1991: 141), after reviewing the type material, stated that Philippi’s *A. araucana*, *A. davilae* and *A. suborbicularis* were all the same species of *Periploma* (*Aelga*), but did not indicate which name was to be used.

#### Cuspidariidae

*kochii*, *Corbula* – Philippi, 1844z4: 70–71, [86], pl. 2, fig. 3. Tertiary of Luithorst [Oligocene]. *Cardiomya* (*Cardiomya*) *kochii* (Philippi, 1844) (Janssen, 1979b: 151–152, pl. 4, figs. 85, 86; Schnetler & Palm, 2008: 24, pl. 2, fig. 10a–b).

#### Poromyidae

*granulata*, *Corbula* “?” – Philippi, 1844z4: 45, [86], pl. 2, fig. 2, non Nyst & Westerdorp, 1839. Tertiary of Freden & Diekholz, Nieder-



sachsen, Germany [Late Oligocene]. Synonym of *Poromya hanleyana* Koenen, 1863 (Janssen, 1979b: 147–147, pl. 4, fig. 82).

#### Verticordiidae

*acuticostatus*, *Hippagus* – Philippi, 1844g: 42, 299, pl. 14, fig. 19a–c (as “fig. 18” in text). Valle Lamati, Calabria, Italy; fossil [Pleistocene]. The eastern and western Atlantic *Verticordia acuticostata* (Philippi, 1844) (Abbott & Dance, 1982: 375; Sabelli et al., 1990: 340; Mikkelsen & Bieler, 2007: 208), or as *Spinosipella acuticostata* (Philippi, 1844) (Huber, 2010: 507, 788; Janssen & Krylova, 2014: 74). Simone & Cunha (2008: 62–64, 76) limited Philippi’s species to the European Pliocene, and described *S. agnes* for the Recent taxon, a conclusion rejected by Huber (2015: 848). Type species (M) of *Iphigenia* O. G. Costa, 1850, *non* Schumacher, 1817 [Donacidae]. (Costa’s proposal was in the form of a *nom. nov.* for *Hippagus* Philippi, 1844, *non* I. Lea, 1833, but Philippi was merely misusing Lea’s taxon, not proposing a new, homonymous name.)

### GASTROPODA

#### Patellidae

*conspicua*, *Patella* – Philippi, 1849v: 71 [13], pl. 3, fig. 1. Gabon, Guinea; Largilliert. Syntype, SMF 313946 (63.6 mm x 50.5 mm x 15.4 mm). Synonym of *Patella nigra* da Costa, 1771 (Sabelli et al., 1990: 120).

*cymbium*, *Patella* – Philippi, 1845i: 60. Strait of Magellan, Chile. Syntype, SMF 313847 (44.6 mm x 28.9 mm x 12.5 mm). Synonym of *Nacella mytilina* (Helbling, 1779) (Powell, 1973: 192, pl. 73, fig. 9, pls. 173, 174).

*decora*, *Patella* – Philippi, 1849i: 162; 1849v: 72 [14], pl. 3, fig. 3. Australia; Largilliert. Synonym of the Indo-Pacific *Cellana radians* (Gmelin, 1791) (Powell, 1973: 180–182, pl. 70, figs. 1–4, pls. 156, 160, 161).

*delesserti*, *Patella* – Philippi, 1849b: 2 [9], pl. 1, fig. 5. Marion Island; Largilliert. Syntype SMF 313925 (24.3 mm x 16.7 mm x 6.1 mm). *Nacella delesserti* (Philippi, 1849) (Powell, 1973: 196, pl. 176, figs. 6, 7).

*diemensis*, *Patella* – Philippi, 1849i: 162. Hobart, Tasmania; Largilliert. Synonym of *Patella peronii* Blainville, 1825 (Powell, 1973: 136–137, pl. 65, figs. 11–13, pls. 109, 113; Wilson, 1993: 37, pl. fig. 12).

*fragilis*, *Patella* – Philippi, 1836a: x, 110, pl. 7, fig. 6a, 6b; 1844g: 84. Sicily, Italy. Syntypes, SMF 313938 (Panormo, n = 2) (22.7 mm x 18.1 mm x 5.6 mm; 18.9 mm x 16.1 mm x 4.0 mm). Synonym of *Patella caerulea* (Linnaeus, 1758) (Priolo, 1951a: 104 [36]; Powell, 1973: 99, pls. 61, 63, 72, 74; Sabelli et al., 1990: 119; Kantor & Sysoev, 2005: 28).

*granulata*, *Patella* – Philippi, 1849i: 162. China; Largilliert. An indeterminate species (Pilsbry, 1892: 156).

*hyalina*, *Patella* – Philippi, 1845i: 59; 1849b: 2 [8], pl. 1, fig. 3. Strait of Magellan, Chile. Syntypes, SMF 313924 (n = 2, larger, 18.0 mm x 11.5 mm x 5.2 mm). Synonym of *Nacella mytilina* (Helbling, 1779) (Powell, 1973: 192, pl. 73, fig. 9, pls. 173, 174; Castellanos & Landoni, 1988: 27).

*limbata*, *Patella* – Philippi, 1849v: 71–72 [13–14], pl. 3, fig. 2. Australia; Largilliert. Synonym of *Cellana solida* (Blainville, 1825) (Powell, 1973: 171–172, pl. 73, figs. 4–6, pl. 148, fig. 1, pl. 150; Wilson, 1993: 36, pl. 1, fig. 22a–c).

*miliaris*, *Patella nigrosquamosa* – Philippi, 1849i: 162–163. Gabon in Guinea; Largilliert. Synonym of *Patella (Scutellastra) natalensis* Krauss, 1848 (Pilsbry, 1892: 103, pl. 13, fig. 65–67).

*orichalcea*, *Patella* – Philippi, 1849i: 163. New Zealand; Largilliert. Probable synonym of the Indo-Pacific *Cellana radians* (Gmelin, 1791) (Powell, 1973: 180–182, pl. 70, figs. 1–4, pls. 156, 160, 161).

*pallescent*, *Patella (Acmaea?)* – Philippi, 1849k: 34–35 [6–7], pl. 2, fig. 4. Locality unknown.

*vitrea*, *Patella* – Philippi, 1845i: 60; 1849b: 2 [8], pl. 1, fig. 4. Strait of Magellan, Chile. Syntype, NHMUK 1923.7.13.57 (40.7 mm x 26.9 mm x 16.0 mm) (although G. Robson did not consider this lot to be a type specimen at the time it was acquired from J. Reissner in 1923); 4 syntypes, SMF 313846 (largest, 26.3 mm x 19.0 mm x 6.7 mm). Synonym of *Nacella mytilina* (Helbling, 1779) (Powell, 1973: 192, pl. 73, fig. 9, pls. 173, 174; Castellanos & Landoni, 1988: 27).

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“*garnoti*, *Patella*” – Philippi, 1836a: x, 111. As “*mihi*” for a transfer of *Pileopsis garnoti* Payraudeau, 1826, to *Patella*.

#### Lottiidae

*discors*, *Patella (Acmaea “?”)* – Philippi, 1849k: 35 [7], pl. 2, fig. 5. Mexico; Liebmann. The



Panamic *Collisella discors* (Philippi, 1849) (Keen, 1971: 324–325, fig. 48).

*elegans*, *Acmaea* – Philippi, 1846h: 24; 1849k: 33–34 [5–6], pl. 2, fig. 2, as *Patella* (*Acmaea*?). Laguayra [La Guayra, Venezuela]; Koch. Synonym of the western Atlantic *Lottia antillarum* G. B. Sowerby I, 1834.

*exilis*, *Acmaea* – Philippi, 1846h: 49–50; 1849k: 35 [7], pl. 2, fig. 6, as *Patella* (*Acmaea*?). “Ad extremitatem australem Americae”. The Chilean *Lottia exilis* (Philippi, 1846) (Forcelli, 2000: 52), or as *Collisella exilis* (Philippi, 1846) (Valdovinos, 1999: 125; Letelier et al., 2003: 60).

*grammica*, *Patella* – Philippi, 1851a: [5]. Replacement name for *Patella lineata* (Philippi, 1846), non Lamarck, 1819, non Klipstein, 1845. Simultaneously misspelled as *Patella “grammia”* by Philippi (1851a: [5]). Synonym of *Lottia variabilis* (G. B. Sowerby I, 1839) (Forcelli, 2000: 53, referring to *Patella lineata* Philippi).

*kochi*, *Patella* – Philippi, 1849b: 2 [8], pl. 1, fig. 1. Locality unknown. Synonym of *Lottia gigantea* (Gray in G. B. Sowerby I, 1834) from California (Pilsbry, 1891c: 66).

*leucophaea*, *Acmaea* – Philippi, 1846h: 22–23; 1849k: 37–38 [9–10], pl. 2, fig. 10, as *Patella* (*Acmaea*?). Chile. Synonym of the Chilean *Scurria variabilis* (G. B. Sowerby I, 1839) (Espoz et al., 2004: 271).

*lineata*, *Acmaea* – Philippi, 1846h: 23–24; 1849k: 33 [5], pl. 2, fig. 1, as *Patella* (*Acmaea*?), non *Patella lineata* Lamarck, 1819, non *P. lineata* Klipstein, 1845; renamed *Patella grammica* Philippi, 1851. Chile. Syntypes, SMF 313906 (n = 3) (largest 17.1 mm x 13.3 mm x 4.7 mm). Synonym of *Lottia variabilis* (G. B. Sowerby I, 1839) (Forcelli, 2000: 53); alternatively, placed in *Patelloida* (Carcelles & Williamson, 1951: 258; Ramírez et al., 2003: 258).

*nisoris*, *Acmaea* – Philippi, 1846h: 49; 1849k: 36 [8], pl. 2, fig. 8, as *Patella* (*Acmaea*?). Chile. Synonym of *Scurria variabilis* (G. B. Sowerby I, 1839) (Espoz et al., 2004: 271), or as a valid species of *Lottia* (Forcelli, 2000: 52), or as *Collisella* (Valdovinos, 1999: 125).

*pediculus*, *Patella* – Philippi, 1846h: 21. Mazatlán, Sinaloa, Mexico. *Collisella pediculus* (Philippi, 1846) (Keen, 1971: 325–326, fig. 50).

*plana*, *Acmaea* – Philippi, 1846h: 22; 1849k: 34 [6], pl. 2, fig. 3, as *Patella* (*Acmaea*?). Central Chile. *Scurria plana* (Philippi, 1846)

(Guzmán et al., 1998: 32; Espoz et al., 2004: 273), or as *Lottia plana* (Philippi, 1846) (Forcelli, 2000: 53), or as *Collisella plana* (Philippi, 1846) (Valdovinos, 1999: 126; Letelier et al., 2003: 61).

*punctatissima*, *Acmaea* – Philippi, 1846h: 23; 1849k: 38 [10], pl. 2, fig. 11; 1860a: 180 [1860b: 161], the latter three references as *Patella* (*Acmaea*). Chile; E. B. Philippi. Synonym of *Scurria parasitica* (d’Orbigny, 1841) (Dall, 1909: 280).

#### Lepetidae

*albescens*, *Acmaea* – Philippi, 1846h: 50; 1849k: 35–36 [7–8], pl. 2, fig. 7, as *Patella* (*Acmaea*?). Central Chile. *Lothia albescens* (Philippi, 1846) (Forcelli, 2000: 57), or *Lepeta albescens* (Philippi, 1846) (Letelier et al., 2003: 61). However, Warén et al. (2011: 4) stated that this species “seems to be based on a young nacellid” (Nacellidae).

*emarginuloides*, *Patella* “?” – Philippi, 1868: 224–225. Strait of Magellan; William [Guglielmo] Acton. Erroneously listed as a junior (!) synonym of *Lothia coppingeri* (E. A. Smith, 1881) by Castellanos & Landoni (1988: 32), Forcelli (2000: 57) and Cárdenas et al. (2008: 207), or as a valid species, *Lepeta emarginuloides* (Philippi, 1868) (Carcelles & Williamson, 1951: 260; Valdovinos, 1999: 126; Letelier et al., 2003: 61), now as *Lothia emarginuloides* (Philippi, 1868) (Warén et al., 2011: 4–6, figs. 5–6, 16–18, 23–26; Güller & Zelaya, 2016b: 323–327). Warén et al. (2011: 4) stated that the “type material” was in the MNHNS, but it was not found in 2014.

#### Pendromidae (= Trachysmatidae)

*delicatum*, *Cyclostoma* “?” – Philippi, 1844g: 222, 303, pl. 28, fig. 3, 3a. Messina, Sicily, Italy; fossil [Plio-Pleistocene]. Type species (M) of *Trachysma* G. O. Sars, 1878. However, this genus was based on a misidentification of the species (Iredale, 1911: 257), and the misidentified taxon was named *Trachysma sarsianum* Thiele, 1912. This was accepted by Warén (1980: 12), but a formal ICZN decision or conservation under ICZN Code Art. 70.3 (1999) is still required (P. Bouchet, pers. commun., June 2013). *Torellia delicata* (Philippi, 1844), northern Atlantic (Bouchet & Warén, 1993: 732–735, figs. 1739–1740, 1743–1745, 1748, 1750–1754; Sysoev, 2014: 140).



## Fissurellidae

- adpersa*, *Fissurella* – Philippi, 1845j: 144; 1845q: 34 [2], pl. 1, fig. 3. Locality unknown. The western Atlantic *Lucapina adpersa* (Philippi, 1845) (Redfern, 2013: 4, fig. 9). Type species (OD) of *Chlamydoglyphus* Pilsbry, 1891.
- alba*, *Fissurella* – Philippi, 1845i: 61; 1845q: 34 [2], pl. 1, fig. 4. Strait of Magellan, Chile. Synonym of the Chilean *Fissurella oriens* G. B. Sowerby I, 1834 (McLean, 1984: 49–52, figs. 176–199; Forcelli, 2000: 47). *Fissurella alba* is the type species (OD) of the useless generic synonym *Corrina* Christiaens, 1973.
- araucanum*, *Scutum* “?” – Philippi, 1887a: 103 [1887b: 97], pl. 13, fig. 13. Lebu, Chile; Volckmann; Tertiary.
- australis*, *Fissurella* – Philippi, 1845i: 61. Strait of Magellan, Chile. Synonym of *Fissurella oriens* G. B. Sowerby I, 1834 (McLean, 1984: 49–52, figs. 176–199).
- cancellata*, *Emarginula* – Philippi, 1836a: x, 114–115, pl. 7, fig. 15a–c; 1844g: 89, 90. Palermo, Sicily, Italy. Also fossil. Syntypes, SMF 313780 (n = 3) (largest, 14.5 mm x 11.2 mm x 6.7 mm); PHB MB Ga. 454 (V) 17 (n = 1, Pozzuoli) (14.9 mm x 12.0 mm x 7.4 mm). Synonym of *Emarginula sicula* Gray, 1825 (Sabelli et al., 1990: 125).
- capuliformis*, *Emarginula* – Philippi, 1836a: x, 116, pl. 7, fig. 12a, 12b. Trepani & Palermo, Sicily, Italy. Synonym of *Emarginula rosea* Bell, 1824 (Sabelli et al., 1990: 125).
- concinna*, *Fissurella* – Philippi, 1845j: 143; 1846a: 66 [4], pl. 2, fig. 5. Chile. Synonym of *Fissurella maxima* G. B. Sowerby I, 1835 (Dall, 1909: 284; McLean, 1984: 25–28, figs. 51–63).
- concolor*, *Fissurella* – Philippi, 1887a: 103 [1887b: 98], pl. 58, fig. 8. Mejillones, Chile; [Tertiary]. *Fissurella concolor* Philippi, 1887; Pliocene (Nielsen, 2013: 38).
- decussata*, *Emarginula* – Philippi, 1844g: 89–90, 301, pl. 19, fig. 15. Lamati, Calabria, Italy; fossil.
- elongata*, *Fissurella* – Philippi, 1845j: 144; 1845q: 33–34 [1–2], pl. 1, fig. 2, *non* M’Coy, 1844. Locality unknown. The western Atlantic *Lucapina philippiana* (Finlay, 1930), *nom. nov.* (Tunnell et al., 2010: 110; Redfern, 2013: 5, fig. 11).
- emarginatus*, *Parmophorus* – Philippi, 1851c: 89. Liew-Kiew Island, China [Ryukyu Islands, Japan]; Largilliert. Synonym of *Tugalina* (*Scelidotoma*) *unguis* (Linnaeus, 1758) (Higo et al., 1999: 41, as “1825”).
- flavida*, *Fissurella* – Philippi, 1855a: 208; 1856c: 100; 1856e: 165. Strait of Magellan, Chile. Synonym of *Fissurella oriens* G. B. Sowerby I, 1834 (McLean, 1984: 49–52, figs. 176–199; Forcelli, 2000: 47, both of whom dated Philippi’s species from 1857).
- gibba*, *Fissurella* – Philippi, 1836a: x, 117–118, pl. 7, fig. 16a–c [not cited in text]; 1844g: 91. Sicily, Italy. Also fossil. Syntypes, SMF 313797 (n = 3) (largest, 11.7 mm x 7.6 mm x 4.9 mm); possible syntypes PHB MB Ga. 12017.1–7 (V) 17 (Palermo, ex Philippi); PHB MB Ga. 12018.1–4 (V) 17 (Palermo, ex Philippi); PHB MB Ga. 12026.1–2 (V) 17 (Pozzuoli, ex Philippi); PHB MB Ga. 12028.1–2 (V) 17 (Molazzo, ex Philippi). Synonym of *Diodora gibberula* (Lamarck, 1822) (Sabelli et al., 1990: 123).
- nigra*, *Fissurella* – Philippi, 1845i: 60–61, 1846a: 65 [3], pl. 2, fig. 2, *non* Lesson, 1831. Chile. Synonym of *Fissurella radiosa* Lesson, 1831; unnecessarily replaced as both *Fissurella philippiana* Reeve, 1850, and as *Fissurella philippii* Hupé, 1854 (Pilsbry, 1890b: 146–147; Castellanos & Landoni, 1988: 12–13; McLean, 1984: 43–49, figs. 147–175).
- punctulata*, *Emarginula* – Philippi, 1844z4: 51, [87], pl. 3, figs. 1, 1a. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Lectotype, RPMH (Hildesheim), from Freden (Philippi’s fig. 1a) (designated by Janssen, 1978b: 143–144, pl. 9, fig. 8); paralectotype (specimen in Philippi’s fig. 1), not found. *Emarginula* (*Emarginula*) *punctulata* (Philippi, 1844) (Anderson, 1959: 42–43, pl. 1, figs. 11–12, pl. 2, fig. 1; Janssen, 1978a: 18, 1978b: 143–144, pl. 9, fig. 8; Rust, 1999: 18–19).
- rueppeli*, *Parmophorus* – Philippi, 1851c: 89, as *P. rüppeli*. Australia. Although the species name is an error, since it was based on the collector Rüppell (single “l” vs. “ll”), ICZN Code Article 32.5.1 (1999) does not apply to require correcting. Not a junior secondary homonym of *Fissurella ruppelli* G. B. Sowerby I, 1834, from the Red Sea (ICZN Code Articles 57–58 (1999)).
- solida*, *Fissurella* – Philippi, 1845j: 142–143. Chile. Synonym of *Fissurella maxima* G. B. Sowerby I, 1834 (McLean, 1984: 25–28, figs. 51–63).
- solida*, *Fissurella* – Philippi, 1847r: 120, *non* Philippi, 1845. Locality unknown.



## Haliotidae

*decussata*, *Haliotis* – Philippi, 1850d: 89–90 [13–14], pl. 9, fig. 2. Locality unknown. Syntype, MNHNS 60.018 (n = 1, “Nueva Hollanda” [= Australia], 53.7 mm x 36.1 mm x 11.4 mm). Synonym of the west African *Haliotis marmorata* Linnaeus, 1758 (Geiger & Owen, 2012: 102–102, fig. 58, pl. 37).

*fulgens*, *Haliotis* – Philippi, 1845w: 150, 1847b: 219 [11], pl. 7, fig. 1, pl. 8, fig. 1. Locality unknown. The northeastern Pacific *Haliotis fulgens* Philippi, 1845; type material unknown (Geiger & Owen, 2012: 90–93, fig. 48, pl. 24, pl. 86, fig. 4, pl. 88, fig. 3).

*gibba*, *Haliotis* – Philippi, 1846b: 70 [8], pl. 4, fig. 2. Australia “?”. Figured syntype, MNHNS 182 (54.9 mm x 39.7 mm x 18.6 mm). Synonym of the New Zealand *Haliotis virginea* Gmelin, 1791 (Geiger & Owen, 2012: 138–139, fig. 89, pl. 75).

*gruneri*, *Haliotis* – Philippi, 1848b: 16; 1850d: 89 [13], pl. 9, fig. 1. China; Gruner. Syntype, MNHNS 200 (64.7 mm x 41.2 mm x 14.3 mm). Fauvel (1880: 197 [245]) erroneously attributed this species to “Reeve, 1846”, and some online sources have repeated this error. Synonym of *H. diversicolor* Reeve, 1846 (D. L. Geiger, pers. comm., 3 Oct. 2016).

*latilabris*, *Haliotis* – Philippi, 1848b: 15–16; 1850d: 91 [15], pl. 9, fig. 5 [as “4” in text]. Locality not stated. Figured syntype, MNHNS 183 (50.7 mm x 37.9 mm x 16.8 mm; from “Liew-Kiew” = Ryukyu Islands, Japan). Synonym of the southeast Asian *Haliotis ovina* Gmelin, 1791 (Higo et al., 1999: 37; Geiger & Owen, 2012: 106–107, fig. 62, pls. 42, 44).

*naevosa*, *Haliotis* – Philippi, 1844r: 147–148 [5–6], pls. 2, 3, ex Martyn 1784 [invalid, ICZN Opinion 456 (1957)]. New Zealand, Australia. Synonym of the Australian *Haliotis rubra* Leach, 1814 (Geiger & Owen, 2012: 118–119, fig. 73, pl. 54). Philippi’s taxon is the type species (OD) of *Notohaliotis* Cotton & Godfrey, 1933.

*neglecta*, *Haliotis* – Philippi, 1848b: 16; 1850d: 91–92 [15–16], pl. 9, fig. 4 [as “5” in text]. Syntypes, MNHNS 60.026 (n = 2; smaller is figured specimen). Sicily, Italy. Geiger (1998: 98) concluded that this was a valid Mediterranean species; subsequently, Geiger & Owen (2001: 130, fig. 82, pl. 65) determined that Philippi’s species is a junior synonym of *H. stomatiaeformis* Reeve, 1846, incorrectly described from New Zealand, but is instead limited to Malta and Sicily, Italy.

*nodosa*, *Haliotis* – Philippi, 1845w: 149; 1847b: 157 [9], pl. 5, fig. 1, pl. 6, fig. 1. Locality unknown. Synonym of the northeastern Pacific *Haliotis corrugata* W. Wood, 1828 (Geiger & Owen, 2012: 77–78, fig. 37, pl. 9, pl. 86, fig. 3, pl. 88, fig. 4).

*sulcosa*, *Haliotis* – Philippi, 1845w: 150, 1847b: 157–158 [9–10], pl. 6, fig. 2. Australia. Possible syntype, MNHNS 185 (71.3 mm x 56.0 mm x 34.6 mm), but this specimen is worn, unlike the fresh specimen illustrated by Philippi, which is also larger in size (D. Geiger, in litt., 7 Feb. 2016). Synonym of the Western Australian *Haliotis roei* Gray, 1826 (Geiger & Owen, 2012: 116–117, fig. 71, pl. 52).

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“*elegans*, *Haliotis*” – Philippi, 1844k: 119, pl. 1, fig. 1. Australia. A junior objective synonym of *H. clathrata* Lichtenstein, 1794, which the ICZN suppressed in order to conserve the widely used name *H. elegans* (ICZN Opinion 1950, 2000). The ICZN mistakenly listed *H. elegans* as by “Philippi, 1844” (as did Wells et al., 2005: 296), whereas it should be attributed to “Koch in Philippi” (as discussed by Geiger & Stewart, 1998: 210).

## Cirridae

*copiapinus*, *Cirrus* – Philippi, 1883: 302 [repr. pp. 4–5], pl. figs. 1, 2. Cerro del Padre, near Manflas, Chile; Triassic or Jurassic.

*martinezi*, *Cirrus* – Philippi, 1883: 302–303 [repr. 5–6], pl. figs. 3, 4. Cerro del Padre, near Manflas, Chile; Triassic or Jurassic.

## Scissurellidae

*plicata*, *Scissurella* – Philippi, 1836a: 187; 1844g: 159, 302, pl. 25, fig. 18. Thapsi [Magnisis] Peninsula, Sicily, Italy. Synonym of *Scissurella costata* d’Orbigny, 1824 (Priolo, 1950: 21–22; Sabelli et al., 1990: 126; Geiger, 2012: 167–185, figs. 69–82); type material not located (Geiger, 2012).

*reticulata*, *Scissurella* – Philippi, 1853d: 38, pl. 6, fig. 11, *nom. nov. pro Scissurella decussata* Audouin, 1826, *non* d’Orbigny, 1824. *Scissurella reticulata* Philippi, 1853 (Geiger, 2012: 291–296, figs. 180–184). Lectotype, MNHN Paris 5278, specimen from the Savigny collection, figured by Bouchet & Danrigal (1982: 14, fig. 62), designated by Yaron (1983: 265), who also designated this as the lectotype of *S. decussata* Audouin, 1826, *non* d’Orbigny,



1824; “the other [three] specimens in this lot thus become paralectotypes.” Yaron (1983: 265) stated that “Suez, at the head of the Gulf of Suez, should be considered the type locality.”

*striatula*, *Scissurella* – Philippi, 1844g: 160, 302, pl. 25, fig. 33 [not cited in text]; 1853c: 37, pl. 6, fig. 9. Magnisi Peninsula, Sicily, Italy. Synonym of *Scissurella costata* d'Orbigny, 1824 (Sabelli et al., 1990: 126; Geiger, 2012: 167–185, figs. 69–82); type material not located (Geiger, 2012). Anistratenko & Starobogatov (1997: 75), in the abstract of a short article on *Scissurella* in the Black Sea, stated that “the neotype of *Scissurella striatula* Phil. is designated,” but the text of their article contains no such designation. Philippi's taxon is the type species (M) of *Schismope* Jeffreys, 1856, a synonym of *Scissurella* d'Orbigny, 1824.

#### Anatomidae

*aspera*, *Scissurella* – Philippi, 1844g: 160, 302, pl. 25, fig. 17, 17a; 1853c: 35–36, pl. 6, fig. 6. Rhegium, Calabria, Italy; fossil. Original type material not located; SBMNH 149681, neotype designated by Høisaeter & Geiger (2011). *Anatoma aspera* (Philippi, 1844) (Giribet & Peñas, 1997: 62 [24]; Geiger, 2012: 774–788, figs. 623–632).

#### Seguenziidae

*reticulatum*, *Solarium* – Philippi, 1844g: 149, 302, pl. 25, fig. 6. Lamati, Calabria, Italy; fossil. *Ancistrobasis reticulata* (Philippi, 1844); Pliocene to Recent (Warén, 1991: 56, fig. 1A, 1996: 206–207).

#### Trochidae

*Cittarium* – Philippi, 1847c: 21, *nom. nov. pro Meleagris* Montfort, 1810, *non* Linnaeus, 1758 [Aves]. Type species: *Turbo pica* Linnaeus, 1758, the type species (OD) of *Meleagris*. Recent, western Atlantic.

*Craspedotus* – Philippi, 1847c: 23, *non* Schoenherr, 1844 [Coleoptera]. Type species (OD): *Monodonta limbata* Philippi, 1844g. Synonym of *Danilia* Brusina, 1865, which has the same type species (Herbert, 2012: 410–412).

*Diloma* – Philippi, 1845a: 188 [22]. Type species (SD Fischer, 1880): *Turbo nigerimus* Gmelin, 1791. Recent, western South America. A valid genus of Trochidae in New Zealand and South America.

*Euchelus* – Philippi, 1847c: 20. Type species (SD Herrmannsen, 1847): *Trochus quadricarinatus* Holten, 1802 (now *Euchelus asper* (Gmelin, 1791). Recent, Indian Ocean. A valid genus of Trochidae (Higo et al., 1999: 52; Herbert, 2012: 425).

*Omphalius* – Philippi, 1847c: 21. Type species (SD Herrmannsen, 1847): *Trochus rusticus* Gmelin, 1791. Recent, Japan. *Neomphalius* P. Fischer, 1885, unnecessary substitute name because it is not preoccupied by *Omphalia* de Haan, 1825 [Cephalopoda] – which has a sufficiently different spelling.

*Osilinus* – Philippi, 1847c: 20. Type species (SD ICZN Opinion 1930, 1999): *Trochus turbinatus* Born, 1778. Recent, Mediterranean. Gofas & Jabaud (1997: 62) discussed the nomenclatural history of this genus. Currently used as a valid subgenus of *Monodonta* Lamarck, 1799 (Sabelli et al., 1990: 135; Herbert, 1994b; Gofas & Herbert, 1998).

*Oxystele* – Philippi, 1847c: 19. Type species (SD Herrmannsen, 1847): *Trochus merula* “Chemn.” Dillwyn, 1817 (= *T. sinensis* Gmelin, 1791) (Herbert, 2015: 55). Recent, Indo-Pacific. Currently used as a valid genus (Herbert, 2015: 55–57).

*adelaidae*, *Trochus* – Philippi, 1851e: 140–141; 1848k: pl. 24, fig. 1. Adelaide, Australia. The uncaptioned plate (1848) appeared three years before the text (1851) making the name available. Syntypes, NHMUK 1923.7.13.61–63 (largest, 13.5 mm x 13.8 mm) (although G. Robson did not consider this lot to be a type specimen at the time it was acquired from J. Reissner in 1923); possible syntypes ZMB 117928 (n = 4). *Austrocochlea adelaidae* (Philippi, 1848) (Wilson, 1993: 75, pl. 7, fig. 7; Wells et al., 2005: 298, both as “1849”).

*adriaticus*, *Trochus* – Philippi, 1844g: 153, 302, pl. 25, fig. 10; 1849z3: pl. 29, fig. 18; 1851e: 194–195. Adriatic Sea. Syntypes, ZMB 112769 (n = 3) (largest, 11.3 mm x 10.6 mm). *Gibbula adriatica* (Philippi, 1844) (Sabelli et al., 1990: 131) or as *Colliculus adriaticus* (Philippi, 1844) (Kantor & Sysoev, 2005: 32, as “*C. adriaticus*”).

*alternatus*, *Trochus* – Philippi, 1849z3: 83–84; 1847z5: pl. 15, fig. 2. Locality unknown. The uncaptioned plate (1847) appeared two years before the text (1849) making the name available.

*altus*, *Trochus* – Philippi, 1851e: 217, *nom. nov. pro Trochus turris* Philippi, 1846i, *non* Pusch, 1837. However, the replacement name is itself a junior homonym of *T. altus* Perry, 1811. Possible synonym of *Trochus*



- conus* Gmelin, 1791 (Pilsbry, 1889a: 18–19, as *T. acutangulus* Chemnitz).
- alveolatus*, *Trochus* – Philippi, 1851e: 207–208; 1849z3: pl. 30, fig. 14. Locality unknown. Probably intended as a replacement name for *Trochus pictus* Philippi, 1846i, *non* W. Wood, 1828, but he did not make this explicit, nor did he cite the earlier homonym, so it has to be taken as a new species. The uncaptioned plate (1849) appeared two years before the text (1851) making the name available. Listed as a possible synonym of *Gibbula* (*Colliculus*) *nivosa* A. Adams, 1851, in Sabelli et al. (1990: 131), whereas Philippi's *Trochus pictus* was listed as a certain synonym. However, they also listed *T. alveolatus* as a possible synonym of *Gibbula* (*Colliculus*) *spratti* (Forbes, 1844) (Sabelli et al., 1990: 132).
- anguliferus*, *Globulus* – Philippi, 1852a: 20; 1853c: 51, pl. 8, fig. 3. Locality unknown.
- Ethalia zelandica* (Hombron & Jacquinot, 1855), New Zealand (Pilsbry, 1890a: 459; Powell, 1979: 65).
- anus*, *Trochus* (*Clanculus*) – Philippi, 1849h: 101; 1849z3: pl. 39, fig. 7; 1855c: 266–267. Locality unknown. *Trochus* (*T.*) *anus* Philippi, 1849, from Australia (Pilsbry, 1889a: 54, pl. 11, figs. 43–45, pl. 14, figs. 34–36), or synonym of *Euriclanculus maxillatus* (Menke, 1843) (Cotton, 1959: 128–129, fig. 64).
- araucanus*, *Trochus* – Philippi, 1887a: 101 [1887b: 96], pl. 12, fig. 3, *non* d'Orbigny, 1838. Near Lebu, Chile; Ovalle; Tertiary. Nielsen et al. (2004: 74) concluded that this was a *nomen dubium*, as the type material was lost.
- articulatus*, *Globulus* – Philippi, 1852a: 20; 1853c: 49–50, pl. 7, figs. 24, 25. Locality unknown. Synonym of *Umbonium sagittatum* (Hinds, 1845) from Indonesia (Pilsbry, 1890a: 452, pl. 59, fig. 47).
- arvensis*, *Trochus* – Philippi, 1847-l: 62, pl. 9, fig. 7. Magdeburg area, Germany; Tertiary; Sack's collection. Possible senior synonym of *Tiburnus margaritula* (Sandberger, 1859) (Anderson, 1959: 55–57, pl. 2, fig. 4).
- aspersus*, *Trochus* – Philippi, 1846i: 103, *ex* Koch ms. Locality unknown; Koch. The Tasmanian *Herpetopoma aspersus* (Philippi, 1846) (Cotton, 1959: 188–189, fig. 117; Wilson, 1993: 68, pl. 10, fig. 4; Wells et al., 2005: 299).
- atrovirens*, *Trochus* – Philippi, 1851e: 148; 1848k: pl. 24, fig. 12. Locality unknown. The uncaptioned plate (1848) appeared three years before the text (1851) making the name available. Synonym of the New Zealand *Diloma* (*Fractarmilla*) *zelandica* (Quoy & Gaimard, 1834) (Powell, 1979: 53, pl. 18, fig. 27).
- australis*, *Globulus* – Philippi, 1852a: 20; 1853c: 48, pl. 7, figs. 21–23. Australia; Gruner. Synonym of *Umbonium vestiarium* (Linnaeus, 1758) (Pilsbry, 1890a: 451).
- balteatus*, *Trochus* – Philippi, 1850: 148; 1850q: pl. 44, fig. 10; 1855c: 307. Locality unknown; Anton coll. *Gibbula balteata* (Philippi, 1850) (Pilsbry, 1890a: 221, pl. 33, fig. 92), or as *Cantharidella balteata* (Philippi, 1850), from Australia (Cotton, 1959: 175–176, fig. 105).
- belcheri*, *Trochus* – Philippi, 1850a: 148–149; 1850q: pl. 44, fig. 3; 1855c: 302–303. Locality unknown; Hanley coll. The southeast Asian *Monilea belcheri* (Philippi, 1850) (Higo et al., 1999: 67; Okutani, 2000: 82–83, fig. 135; Swennen et al., 2001: 107, fig. 269, as “1849”; Wilson, 1993: 94, pl. 11, figs. 20a, b).
- bembex*, *Trochus* – Philippi, 1855c: 286; 1850q: pl. 42, fig. 5, *nom. nov. pro Margarita acuminata* G. B. Sowerby I, 1838, *non Trochus acuminatus* W. Wood, 1828, when Philippi placed both species in *Trochus*. Locality unknown. Synonym of the Arctic *Margarita acuminata* (G. B. Sowerby I, 1838) (Pilsbry, 1890a: 287).
- biasoletti*, *Trochus* – Philippi, 1836a: 178–179, footnote, pl. 10, fig. 18; 1849z3: pl. 29, fig. 1; 1851e: 187–188. Trieste or Livorno. In 1851, Philippi disclaimed his 1836 figure. Syntypes, ZMB 12170 (n = 5, Trieste) (largest, 22.8 mm x 22.5 mm). Synonym of *Gibbula* (*Gibbula*) *albida* (Gmelin, 1791) (Sabelli et al., 1990: 130).
- bicinctus*, *Trochus* (*Phorcus*) – Philippi, 1849h: 102; 1849z3: pl. 35, fig. 2; 1851e: 230–231. Red Sea; Hemprich & Ehrenberg. Herbert (1994a: 147–148, fig. 16), determined that most records from the Persian Gulf and Red Sea attributed to this species were actually *Clanculus gennesi* H. Fischer, 1901, and that Philippi's species is best treated as a *nomen dubium*.
- bilabiatus*, *Trochus* – Philippi, 1852d: 240–241; 1849z3: pl. 36, fig. 10, *nom. nov. pro Trochus limbatus* (Philippi, 1844g), *non* Quoy & Gaimard, 1834. The uncaptioned plate (1849) appeared three years before the text (1852) making the name available. Synonym of *Danilia otaviana* (Cantraine, 1835) (Sabelli et al., 1990: 134, as “1847”) or of *D. tineia* (Calcara, 1839) (Priolo, 1951a: 111–112 [43–44]).
- borealis*, *Trochus* – Philippi, 1855c: 283–284; 1850q: pl. 42, fig. 1. Spitzbergen; Kröyer & Maine; Griffith. The uncaptioned plate (1850)



- appeared five years before the text (1855) making the name available. Synonym of *Margarita helicina* (Fabricius, 1780) (Pilsbry, 1890a: 286).
- brunneus*, *Trochus* (*Chlorostoma*) – Philippi, 1849q: 188; 1850q: pl. 43, fig. 19; 1855c: 300–301. Locality unknown. *Tegula brunnea* (Philippi, 1849), from California (Abbott, 1974: 50), or *Chlorostoma brunnea* (Philippi, 1849) (McLean, 2007: 724).
- bullatus*, *Trochus* – Philippi, 1844g: 226, 303, pl. 28, fig. 8. Messina, Sicily, Italy; Pleistocene; A. G. Otto. Syntypes, PHB MB Ga. 444 (n = 4) (the most intact specimen is 28.4 mm x 31.6 mm; others are fragmented).
- callichrous*, *Trochus* – Philippi, 1850a: 149–150; 1850q: pl. 43, fig. 18; 1855c: 300. Locality unknown; Hanley coll. The Japanese *Cantharidus callichroa* (Philippi, 1850) (Higo et al., 1999: 59; Okutani, 2000: 66–67, fig. 68).
- callicoccus*, *Trochus* – Philippi, 1850a: 150–151; 1850q: pl. 43, fig. 15; 1855c: 298. Locality unknown; Hanley coll. Holotype, NHMUK 1909.5.17.11 (24.8 mm x 31.0 mm). Synonym of *Trochus maculatus* (Linnaeus, 1758), from the Indo-Pacific (Pilsbry, 1889a: 22).
- caperatus*, *Trochus* – Philippi, 1849z3: 107; 1847z5: pl. 17, fig. 7. Locality unknown. The uncaptioned plate (1847) appeared two years before the text (1849) making the name available. Synonym of *Trochus fenestratus* Gmelin, 1791, from the Indo-Pacific (Pilsbry, 1889a: 22, as “*caparatus*”).
- capillaceus*, *Trochus* (*Osilinus*?) – Philippi, 1849h: 102–103; 1850q: pl. 40, fig. 7; 1855c: 275. “Nova Hollandia”; Largilliert (stated to be “Auckland Islands”; Marshall, 1998: 130). Syntypes, MNHN Paris (n = 2) (21.5 mm x 16.7 mm; 21.6 mm x 15.2 mm); Muséum de Rouen 168801083 (n = 3) (largest 24.5 mm x 18.4 mm). *Cantharidus* (*Plumbelenchus*) *capillaceus* (Philippi, 1849), restricted to Macquarie, Auckland, Campbell and Antipodes Islands, southern New Zealand (Powell, 1979: 55, pl. 18, fig. 4; Marshall, 1998: 130). Type species (OD) of *Plumbelenchus* Finlay, 1926.
- carbonarius*, *Trochus* (*Diloma*) – Philippi, 1849h: 103; 1850q: pl. 40, fig. 9; 1855c: 276–277. King George Sound, Western Australia. *Monodonta carbonaria* (Philippi, 1849) (Pilsbry, 1889a: 105–106, pl. 34, fig. 30), or possibly a synonym of *Fractarmilla rudis* (Gray, 1826) (Cotton, 1959: 164–165, fig. 95).
- chlorites*, *Trochus* – Philippi, 1848k: 60; 1847z5: pl. 13, fig. 2, *nom. nov. pro Trochus viridulus* Menke, 1843, *non* Gmelin, 1791. The uncaptioned plate (1847) appeared one year before the text (1848) making the name available. West coast of Australia; Preiss. *Prothalotia chlorites* (Philippi, 1848).
- cinctus*, *Trochus* – Philippi, 1836a: xii, 185, pl. 10, fig. 20, 20a; 1844g: 157. Militello, Sicily, Italy; fossil. *Solariella cincta* (Philippi, 1836) (Landau et al., 2003: 61–62, pl. 15, fig. 5; Sysoev, 2014: 137). Holotype, PHB MB Ga. 461 (6.7 mm x 7.7 mm) (Warén, 1993: 161, fig. 1B, 1C). Warén determined that Philippi’s species, from Plio-Pleistocene deposits, was long erroneously considered to be a senior synonym of the Recent *Solariella amabilis* (Jeffreys, 1865), and concluded that they are not conspecific.
- concinus*, *Trochus* – Philippi, 1846i: 105–106; 1847z5: pl. 16, fig. 1; 1849z3: 94–95. Locality unknown; Stuttgart coll.
- concolor*, *Trochus magus* var. – Philippi, 1836a: 181, as var. “concolorem, fuscam...” Locality presumably Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1885: 378, pl. 45, figs. 3–4), as *Trochus magus* var. *concolor* Philippi, 1836.
- corvus*, *Trochus* – Philippi, 1850a: 152. Western South America; Jonas; Hamburg Museum. *Tegula* (*Agathistoma*) *corvus* (Philippi, 1850), from Peru (Ramírez et al., 2003: 258).
- crinitus*, *Trochus* (*Phorcus*) – Philippi, 1849h: 103–104; 1849z3: pl. 35, fig. 9; 1852d: 235. Australia; Largilliert. Type species of *Chlorodiloma* Pilsbry, 1889. *Austrocochlea crinita* (Philippi, 1849) (Wilson, 1993: 75, pl. 7, fig. 8a, b; Wells et al., 2005: 298).
- crispula*, *Delphinula* – Philippi, 1841f: 21–22; 1844z4: 21–22, [87], pl. 3, fig. 31. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Nomen dubium*, or possibly conspecific with *Delphinula suturalis* Philippi, 1844 (Janssen, 1978b: 146), in which case it would be the older name. Type material lost (R. Janssen, pers. comm., April 2013).
- crispulus*, *Trochus* – Philippi, 1844g: 156, 302, pl. 25, fig. 12. Rhegio, Calabria, Italy; fossil. Possible synonym of *Putzeysia wiseri* (Calcar, 1842) (Sabelli et al., 1990: 134).
- cruentus*, *Trochus* – Philippi, 1844p: 140 [18], pl. 4, fig. 4; 1849z3: pl. 25, fig. 10; 1851e: 157–158. Locality unknown. *Chlorostoma cruentum* (Philippi, 1844), from China (Yen, 1942: 178).
- dama*, *Trochus* (*Labio*) – Philippi, 1849h: 105; 1849z3: pl. 35, fig. 6; 1852d: 233. Red Sea; Hemprich & Ehrenberg. Syntypes, ZMB



- 117927 (n = 10) (largest 23.5 mm x 21.6 mm). The Red Sea *Monodonta dama* (Philippi, 1849) (Abbott & Dance, 1982: 41).
- decoratus*, *Trochus* – Philippi, 1846i: 102; 1847z5: pl. 13, fig. 1; 1848k: 59. Locality unknown; Gruner. *Cantharidus* (*Prothalotia*) *decoratus* (Philippi, 1846), from Western Australia (Thiele, 1930: 566), or a synonym of the Indo-Pacific *Odontotrochus indistinctus* (W. Wood, 1828).
- delicatulus*, *Trochus* – Philippi, 1846i: 105; 1849z3: pl. 28, fig. 1; 1851e: 176. Pacific Ocean; Gruner. Syntype, ZMB 29935 (6.3 mm x 9.5 mm). Possible synonym of *Trochus* (*Coelotrochus*) *tiaratus* (Quoy & Gaimard, 1834) (Marshall, 1998: 75–76, figs. 1–4, 9, 12).
- elevatum*, *Solarium* – Philippi, 1845z: 449 [*nomen nudum*]; 1847-l: 61, pl. 9, fig. 2a–c. Magdeburg area, Germany; Tertiary; Sack's collection. Type material in PHB MB Ga. — (R. Janssen, in litt., 9 Feb. 2016). *Margarita elevatum* (Philippi, 1847); Oligocene of northern Germany (Koenen, 1892: 873–875, pl. 56, figs. 5, 7).
- elevatus*, *Trochus* – Philippi, 1844g: 155, footnote, 302, pl. 25, fig. 9. Vicentia, Italy; fossil [Tertiary]. *Periaulax elevata* (Philippi, 1844) (Amitrov, 2009: 386).
- erubescens*, *Trochus* – Philippi, 1849z3: 101–102; 1847z5: pl. 16, fig. 13. Locality unknown. The uncaptioned plate (1847) appeared two years before the text (1849) making the name available. Probable synonym of *Clanculus kraussi* (Philippi, 1846), from the eastern Atlantic (Pilsbry, 1889a: 73, pl. 42, figs. 12, 13, “seems to be a variety”).
- eucosmus*, *Trochus* (*Polydonta*) – Philippi, 1849h: 104; 1849z3: pl. 38, fig. 11; 1855c: 260–261. Locality unknown. Synonym of *Trochus radiatus* Gmelin, 1791, from the Indo-Pacific (Pilsbry, 1889a: 37).
- eugrammus*, *Trochus* – Philippi, 1850a: 153; 1850q: pl. 43, fig. 17; 1855c: 299–300. Locality unknown; Hanley coll. Synonym of *Trochus lineatus* Lamarck, 1822, from the Indo-Pacific (Pilsbry, 1889a: 33).
- euomphalus*, *Trochus* – Philippi, 1836a: xii, 184–185, pl. 10, fig. 21; 1844g: 156. Militello, Sicily, Italy; fossil. Holotype, PHB MB Ga. 451 (32.4 mm x 29.0 mm). *Gibbula euomphala* (Philippi, 1836), Pliocene (Forli et al., 2014).
- eustephes*, *Trochus* – Philippi, 1850a: 153–154; 1850q: pl. 43, fig. 6; 1855c: 293. Locality unknown; Hanley coll. Probable syntype, NHMUK 1909.5.17.2 (15.9 mm x 20.7 mm).
- Pilsbry (1889a: 28) listed this as a synonym of *Trochus incrassatus creniferus* Kiener, 1850, from the Indo-Pacific; however, Philippi's name was published in March 1850, whereas Kiener's name was published in “1850” (i.e., December 1850), so Philippi's name has priority.
- exaltatus*, *Trochus* – Philippi, 1849z3: 108; 1847z5: pl. 17, fig. 8. Locality unknown. The uncaptioned plate (1847) appeared two years before the text (1849) making the name available. Synonym of the Indo-Pacific *Trochus fenestratus* Gmelin, 1791 (Pilsbry, 1889a: 22).
- exilis*, *Trochus* – Philippi, 1844g: 156, 302, pl. 25, fig. 15, 15a. Palermo, Sicily, Italy; fossil [subsequently reported from the Recent fauna]. Clark (1859) discussed the differences between this species and his own *Trochus cutlerianus* Clark, 1849.
- fabricii*, *Trochus* – Philippi, 1855c: 284; 1850q: pl. 42, fig. 2. Greenland, Fabricius & Spitzbergen, Kröyer. The uncaptioned plate (1850) appeared five years before the text (1855) making the name available. Synonym of *Margarites groenlandicus* (Gmelin, 1791) (Kantor & Sysoev, 2005: 33–34).
- festivus*, *Trochus* – Philippi, 1849z3: 116; 1848k: pl. 19, fig. 5. Locality unknown. The uncaptioned plate (1848) appeared one year before the text (1849) making the name available. Synonym of *Trochus radiatus* Gmelin, 1791, from the Indo-Pacific (Pilsbry, 1889a: 37).
- filosus*, *Trochus* – Philippi, 1844g: 155–156, 302, pl. 25, fig. 24. Lamati & Taranto, Calabria, Italy; fossil. Presumably a synonym of the Pleistocene to Recent Mediterranean *Cantrainea peloritana* (Cantraine, 1835) (Smriglio et al., 1992).
- firmus*, *Trochus* – Philippi, 1850a: 155; 1850q: pl. 45, fig. 5; 1855c: 317. Persia; Hamburg Museum. *Trochus* (*Infundibulops*) *firmus* Philippi, 1850 (Pilsbry, 1890a: 467; Bosch et al., 1995: 34, fig. 39).
- flagellatus*, *Trochus* (*Clanculus*) – Philippi, 1849h: 105; 1849z3: pl. 39, fig. 9; 1855c: 267–268. Locality unknown. The South Australian and Tasmanian *Clanculus flagellatus* (Philippi, 1849) (Cotton, 1959: 127–128, fig. 63; Wilson, 1993: 86, pl. 8, fig. 9a, b; Wells et al., 2005: 298); type species (OD) of *Euriclanculus* Cotton & Godfrey, 1934.
- floridus*, *Trochus* – Philippi, 1850a: 156; 1852d: 243; 1849z3: pl. 36, fig. 15. Australia. The uncaptioned plate (1849) appeared one year before the text (1850) making the name



- available. *Clanculus floridus* (Philippi, 1850) (Wilson, 1993: 86, pl. 8, fig. 18a, b).
- fricki*, *Trochus* – Philippi, 1887a: 101 [1887b: 95–96], pl. 12, fig. 7. Llancahue, Chile, Wilhelm Frick; Tubul, Chile; Volckmann; Navidad, Chile; all Tertiary [Miocene]. Syntype, SGO. Pl.813 (labeled as “lectotipo”). Synonym of *Astele chilensis* (d’Orbigny, 1852) (Nielsen et al., 2004: 84–86, figs. 60–69; Griffin & Nielsen, 2008: 299, pl. 21, figs. 4–6).
- fulguratus*, *Trochus* (*Oxysteles*) – Philippi, 1849h: 106; 1849z3: pl. 39, figs. 10, 11; 1855c: 268. Gabon-Guinea. Synonym of *Oxysteles variegata* (Anton, 1839) from western and southern Africa (Kensley & Penrith, 1972), or a valid species of *Oxysteles* from southern Angola (Herbert, 2015: 57, fig. 7-l).
- fumosus*, *Trochus* – Philippi, 1850a: 156–157; 1850q: pl. 44, fig. 5; 1855c: 304. Locality unknown; Hanley coll. Synonym of *Gibbula cineraria* (Linnaeus, 1758), from the eastern Atlantic (Pilsbry, 1889a: 208 (as junior synonym); 1890a: 209 (as a “var.”)).
- fuscescens*, *Trochus* – Philippi, 1844c: 92 [14], pl. 3, fig. 8; 1849z3: pl. 28, fig. 10; 1851e: 182. Chile; E. B. Philippi. Synonym of *Tegula patagonica* (d’Orbigny, 1836) (Forcelli, 2000: 62, as “*T. fuscescens*” and as 1845; Ramírez et al., 2003: 258).
- gaimardi*, *Trochus* – Philippi, 1851e: 211–212; 1849z3: pl. 31, figs. 7–9. Replacement name for *Trochus cingulatus* Quoy & Gaimard, 1834 (p. 259, pl. 64, figs. 16–20), *non* Brocchi, 1814, *non* Megerle von Mühlfeld, 1816, *non* Menke, 1828. French Pass, New Zealand. Syntypes MNHN Paris (n = 5) (of *T. cingulatus* Quoy & Gaimard, 1834). Synonym of the New Zealand *Diloma* (*Fractarmilla*) *bicanaliculata* (Dunker, 1844) (B. Marshall, pers. comm., May 2013); species discussed by Powell (1979: 54, pl. 18, fig. 24).
- gemmulatus*, *Trochus* – Philippi, 1844g: 226, 303, pl. 28, fig. 5, 5a. Messina, Sicily, Italy; Pleistocene; A. G. Otto.
- gilvus*, *Trochus* – Philippi, 1850a: 157–158; 1850q: pl. 43, fig. 6; 1855c: 293. Locality unknown; Hanley coll. *Cantharidus gilvus* (Philippi, 1850) (Pilsbry, 1889a: 147, pl. 51, fig. 15), locality presumably in the Indo-Pacific.
- glabratus*, *Trochus* – Philippi, 1844g: 226–227, 303, pl. 28, fig. 10, 10a. Messina, Sicily, Italy; Pleistocene; A. G. Otto. Presumably synonym of the Pleistocene to Recent Mediterranean *Cantrainea peloritana* (Cantraine, 1835) (Smriglio et al., 1992).
- glabratus*, *Trochus* – Philippi, 1845z: 449 [*nomen nudum*], *non* Philippi, 1844. Germany; fossil.
- glomus*, *Monodonta* – Philippi, 1844g: 157, 158, 302, pl. 25, fig. 16; 1847z5: pl. 14, fig. 15; 1849z3: 82, as *Trochus glomus*. Sicily, Italy. Syntypes, PHB MB Ga. 449 (V) 44 (9.5 mm x 10.6 mm); PHB MB Ga. 446 (V) 44 (9.5 mm x 10.6 mm). Synonym of *Clanculus jussieui* (Payraudeau, 1826) (Priolo, 1953a: 96–98 [94–96], pl. 4, figs. 14–15; Sabelli et al., 1990: 127).
- gracilis*, *Trochus* – Philippi, 1851e: 140–141; 1848k: pl. 23, fig. 20, ex Anton ms, *non* Koch & Dunker, 1837 (fossil) Adelaide, Australia. The uncaptioned plate (1848) appeared three years before the text (1851) making the name available. Philippi indicated that this species was “in literis”, so he is here given credit for the species. Synonym of the Indo-Pacific *Phasianotrochus eximius* (Perry, 1811) (Cotton, 1959: 106, who incorrectly attributed Philippi’s species to “Anton, 1846”).
- gratus*, *Trochus* – Philippi, 1851b: 42–43; 1851e: pl. 46, fig. 4; 1855c: 322–323. Locality unknown.
- grayanus*, *Trochus* – Philippi, 1855c: 281; 1850q: pl. 41, fig. 6, *nom. nov. pro Trochus bicarinatus* Gray, in Griffith & Pidgeon, 1833, *non* Lamarck, 1804, *non* J. Sowerby, 1818, *non* Borson, 1825. The uncaptioned plate (1850) appeared five years before the text (1855) making the name available. Synonym of *Gibbula* (*Gibbula*) *magus* (Linnaeus, 1758) (Priolo, 1951b: 265–266 [57–58]; Sabelli et al., 1990: 131).
- gruneri*, *Trochus* (*Phorcus*) – Philippi, 1849h: 107–108; 1849z3: pl. 28, fig. 13; 1851e: 183–184. Antilles; Gruner. *Tegula gruneri* (Philippi, 1849) (Redfern, 2013: 26, fig. 68).
- gundlachii*, *Trochus* (*Phorcus*) – Philippi, 1849h: 108; 1849z3: pl. 34, fig. 13; 1851e: 226. Cuba; E. B. Philippi & Gundlach. Synonym of *Tegula lividomaculata* (C. B. Adams, 1845) (Abbott, 1958: 26–27; 1974: 50).
- guttadauri*, *Trochus* – Philippi, 1836a: xii, 182, pl. 11, fig. 1; 1844g: 154, 156; 1849z3: pl. 28, fig. 6; 1851e: 179. Castello, Sicily, Italy. Also fossil. Syntype, ZMB 11997. *Gibbula* (*Forskalea*) *guttadauri* (Philippi, 1836) (Priolo, 1951b: 285 [77]; Sabelli et al., 1990: 13, 132); *Gibbula guttadauri* (Philippi, 1836) (Giribet & Peñas, 1997: 47 [9]). Type species (OD) of *Gibboforskalia* Coen, 1937, an overlooked taxon.
- guttatus*, *Trochus* – Philippi, 1846i: 104, ex Koch ms. Locality unknown; Koch.



- helicoides*, *Trochus adansonii* var.  $\beta$  [beta] – Philippi, 1836a: 182, pl. 10, fig. 24; 1849z3: pl. 29, fig. 23; 1851e: 197. Adopted as the valid name of a species pursuant to ICZN Code Article 45.6.4.1 (1999) by Philippi (1851e: 197), as *T. helicoides*. Sicily, Mediterranean. Syntypes ZMB 12198 (n = 2, larger, 7.8 mm x 7.0 mm). Synonym of *Gibbula* (*Colliculus*) *turbinoides* (Deshayes, 1835) (Priolo, 1951b: 270–271 [62–63], pl. 2, fig. 9; Sabelli et al., 1990: 132).
- horridus*, *Trochus* (*Euchele*) – Philippi, 1849h: 108; 1849z3: pl. 27, fig. 12; 1851e: 172–173. Pacific Ocean; E. B. Philippi. *Euchelus horridus* (Philippi, 1849) (Pilsbry, 1890a: 433, pl. 37, fig. 17; Jansen, 1994: 56–57, pl. 1, figs. 1–2), from the Indo-Pacific.
- ignobilis*, *Trochus* – Philippi, 1846i: 102. Hawaii; Bronn. Possible senior synonym of *Trochus intextus* Kiener, 1850 (Kay, 1979: 50, 52, fig. 14F, G).
- incarnatus*, *Trochus* – Philippi, 1846i: 103; 1847z5: pl. 16, fig. 3; 1849z3: 96–97. Locality unknown; Stuttgart coll. *Trochus maculatus* var. *incarnatus* Philippi, 1846, from the Indo-Pacific (Pilsbry, 1889a: 26, pl. 8, figs. 80–81).
- indecorus*, *Trochus* – Philippi, 1846i: 104–105; 1848k: pl. 24, fig. 5; 1851e: 143. Locality unknown. *Monodonta sauciata* (Koch, 1845), from the eastern Atlantic (Pilsbry, 1889a: 114; Herbert, 2015: 55, fig. 7A).
- infuscatus*, *Trochus* – Philippi, 1851b: 43–44; 1851e: pl. 46, fig. 15; 1855c: 329–330. Locality unknown. Synonym of *Trochus radiatus* Gmelin, 1791, from the Indo-Pacific (Pilsbry, 1889a: 37).
- insularis*, *Trochus* – Philippi, 1887a: 100 [1887b: 94], pl. 11, fig. 21. Isla Quiriquina, Chile; Cretaceous. Syntypes, SGO.PI.820 (labeled as “lectotipo”); SGO.PI.4678–4680 (each labeled as “paralectotipo”). *Solariella unio* (Philippi, 1887) (Wilckens, 1904: 194–195).
- jonasii*, *Trochus* (*Polydonta*) – Philippi, 1849h: 108–109; 1849z3: pl. 38, figs. 9, 10; 1855c: 260. Locality unknown. Synonym of *Trochus maculatus* Linnaeus, 1758, from the Indo-Pacific (Pilsbry, 1889a: 25).
- kochii*, *Trochus* – Philippi, 1844p: 138 [16], pl. 4, fig. 8; 1847z5: pl. 17, fig. 3; 1849z3: 104, as *T. “kochi.”* Locality unknown. The Indian Ocean *Trochus* (*Infundibulops*) *kochii* Philippi, 1844 (Bosch et al., 1995: 35, fig. 41; Marshall, 2000: 150–151, figs. 8, 10).
- kotschyi*, *Trochus* (*Polydonta*) – Philippi, 1849h: 127; 1849z3: pl. 35, fig. 8; 1852d: 234–235. Karak, Perisco; Kotschy. *Osilinus kotschyi* (Philippi, 1849), from the Persian Gulf, Gulf of Oman, Arabian Sea, and Red Sea (Herbert, 1994b; Bosch et al., 1995: 36, fig. 47).
- kraussii*, *Monodonta* – Philippi, 1846i: 100; 1847z5: pl. 14, fig. 14; 1849z3: 82–83. Locality unknown; Krauss. The eastern Atlantic *Clanculus kraussii* (Philippi, 1846) (Nicklès, 1950: 43–44, fig. 26, as *C. “kraussi”*). Neotype, ZMB 104022 (Dakar, Senegal) (10.3 mm x 11.0 mm), designated by Rubio & Rolán (2002: 35, figs. 55–57, 133–134). Herbert (1993a: 252–253) had determined that records from southern Africa of this tropical west African species were misidentifications of *Clanculus atricatena* Tomlin, 1921.
- lactea*, *Monodonta* – Philippi, 1845i: 66; 1847z5: pl. 14, fig. 16; 1849z3: 83, as *Trochus lacteus*. Insulae Amicorum [Tonga]. *Euchelus lacteus* (Philippi, 1845) (Pilsbry, 1890a: 442, pl. 57, figs. 37–38).
- laetus*, *Trochus* – Philippi, 1850q: 133–134; 1848k: pl. 23, fig. 6. Australia. The uncaptioned plate (1848) appeared two years before the text (1850) making the name available. Synonym of *Phasianotrochus irisodontes* (Quoy & Gaimard, 1834), from southern Australia (Pilsbry, 1889a: 133).
- largillierti*, *Trochus* (*Clanculus*) – Philippi, 1849h: 109; 1849z3: pl. 39, fig. 6; 1855c: 265–266. Locality unknown; Largilliert. Type material not found in MNHN Paris, Muséum de Rouen or ZMB; neotype NMSAL150/T852 (Cap la Houssaye, Réunion), designated by Herbert (1993b: 314, figs. 1–4). *Clanculus* (C.) *largillierti* (Philippi, 1849), known only from the Mascarene Islands of Mauritius and Réunion (Herbert, 1993b).
- laticus*, *Trochus chlorostomus* – Philippi, 1850a: 152. Locality presumably Australia, the locus of *Odonototrochus chlorostoma* (Menke, 1843) (Cotton, 1959: 123, as “a wide form” of Menke’s species).
- leachii*, *Trochus* – Philippi, 1852d: 247–248; 1849z3: pl. 36, fig. 6, *nom. nov. pro Trochus striatus* (Leach, 1819), *non Trochus striatus* Linnaeus, 1758. The uncaptioned plate (1849) appeared three years before the text (1852) making the name available. Synonym of *Margarites groenlandicus* (Gmelin, 1791) (Kantor & Sysoev, 2005: 33–34).
- lepidus*, *Trochus* (*Margarita*) – Philippi, 1893b: 7, pl. 1, fig. 13, *non* de Koninck 1843, *non* Koch in Philippi, 1849. Argentina; Tertiary. “*Calliostoma*” *lepidus* (Philippi, 1893), Miocene (Ihering, 1907: 364; Martínez et al., 1998: 28–29, pl. 15, fig. 13).



- leprosus*, *Trochus* – Philippi, 1851b: 40–41; 1851e: pl. 46, fig. 13; 1855c: 328, *non* Morton, 1834. Locality unknown; Ettmüller coll. *Monodonta leprosus* (Philippi, 1851), of unknown locality (Pilsbry, 1889a: 100–101, pl. 34, fig. 23). *Trochus leprosus* Morton, 1834, is a Cretaceous fossil now classified in *Xenophora* (Xenophoridae) (Ponder, 1983: 4, 11, 70).
- leucophaeus*, *Trochus* – Philippi, 1836a: xii, 182, pl. 11, fig. 17; 1844g: 153; 1849z3: pl. 29, fig. 19; 1851e: 195. Ognina, Catania, Sicily, Italy. Syntypes, SMF 314069 (n = 5) (Sicily and Cette). *Gibbula* (*Phorcus*) *leucophaea* (Philippi, 1836) (Priolo, 1951b: 275 [67], pl. 2, fig. 12); *Gibbula leucophaea* (Philippi, 1836) (Sabelli et al., 1990: 132; Giribet & Peñas, 1997: 47 [9]); *Gibbula delicata* Coen, 1937, ex Monterosato ms, is a synonym (Smriglio et al., 1991: 64).
- leucostigma*, *Trochus* – Philippi, 1845r: 38–39 [34–35], pl. 7, fig. 7, ex Menke ms. Australia “?”. A variety of the Australian *Phasianotrochus eximius* (Perry, 1811) (Cotton, 1959: 105–106, fig. 48).
- limbata*, *Monodonta* – Philippi, 1844g: 157, 158, 302, pl. 25, fig. 19 [not “17” as in text], *non Trochus limbatus* Quoy & Gaimard, 1834. Palermo, Sicily, Italy. Renamed *Trochus bilabatus* Philippi, 1852d, when he transferred it to *Trochus*. Type species (M) of *Danilia* Brusina, 1865, which is the next available name for *Craspedotus* Philippi, 1847 *non* Schoenherr, 1844. Synonym of *Danilia otaviana* (Cantraine, 1835) (Sabelli et al., 1990: 134), or of *D. tineia* (Calcara, 1839) (Priolo, 1951a: 111–112 [43–44]; Herbert, 2012: 411).
- lineatus*, *Trochus* (*Margarita*?) – Philippi, 1845i: 66, *non* da Costa, 1778; 1855c: 250, as a synonym of *Margarita caerulea* King, 1832. Strait of Magellan, Chile. Synonym of *Photinula caerulea* (King, 1832) (Castellanos & Landoni, 1989: 22).
- lividus*, *Trochus* – Philippi, 1850a: 168; 1850q: pl. 45, fig. 8; 1855c: 319–322, *non* Kiener, 1850. Locality unknown; Hamburg Museum. Note that Philippi’s name was published in March 1850, whereas Kiener’s name is only “1850” (and hence December 1850), so that Philippi’s name has priority.
- lugubris*, *Trochus* – Philippi, 1844c: 91–92 [13–14], pl. 3, fig. 7; 1849z3: pl. 30, fig. 6; 1851e: 203, *non* Gmelin, 1791. Chile; E. B. Philippi. Dall (1909: 239) listed this as *Tegula lugubris* (Philippi, 1844), but it is a junior homonym and does not appear to have been renamed or have any junior synonyms.
- macsporrani*, *Trochus* – Philippi, 1887a: 102 [1887b: 96], pl. 12, fig. 6, as *T. mac-sporrani*. Isla Santa Margarita; Tertiary. Holotype, SGO.PI.812. Nielsen et al. (2004: 74) determined that the holotype was “an unidentifiable internal mold.”
- margaritaria*, *Monodonta* – Philippi, 1846i: 100–101; 1847z5: pl. 14, fig. 4; 1849z3: 74–75, as *Trochus margaritarius*. Locality unknown; Gruner. The western Pacific *Clanculus margaritarius* (Philippi, 1846) (Abbott & Dance, 1982: 43; Higo et al., 1999: 57; Okutani, 2000: 62–63, fig. 47; Qi, 2004: 18, pl. 8E). Wilson (1993: 89, pl. 8, fig. 3a, b) mistakenly placed it as a junior synonym of *Clanculus unedo* A. Adams, 1853.
- marginulatus*, *Trochus* – Philippi, 1844g: 227, 303, pl. 28, fig. 4, 4a. Messina, Sicily, Italy; Pleistocene; A. G. Otto. *Solariella marginulata* (Philippi, 1844) (Di Geronimo & La Perna, 1997: 396, pl. 1 = p. 397, figs. 6, 7).
- melanchlorus*, *Trochus* – Philippi, 1851e: 220, pl. 33, fig. 2. Australia. Synonym of *Monodonta australis* (Lamarck, 1822) (Pilsbry, 1889a: 88).
- menkeanus*, *Trochus* – Philippi, 1844c: 91 [13], pl. 3, fig. 6; 1855c: 287–288, as a synonym of *Trochus zonatus* W. Wood, 1828. Cape of Good Hope. Synonym of *Gibbula zonata* (W. Wood, 1828) (Herbert, 2015: 53–54).
- metaformis*, *Trochus* – Philippi, 1850a: 168–169; 1850q: pl. 43, fig. 13; 1855c: 296–297. Locality unknown; Hanley coll. *Trochus metaformis* Philippi, 1850 (Pilsbry, 1890a: 475, pl. 67, fig. 53).
- middendorffii*, *Trochus* – Philippi, 1855c: 337, *nom. nov. pro Trochus modestus* Middendorff, 1849, *non* Reeve, 1843, and *non* Koch, 1845. However, Pilsbry (1890a: 293) noted that *Margarita schantarica* Middendorff, 1851, is the next available name for *T. modestus* Middendorff. Pilsbry erroneously stated that *T. modestus* Middendorff “is preoccupied by Philippi” instead of recognizing that Philippi had created an unneeded replacement name.
- millegranus*, *Trochus* – Philippi, 1836a: xii, 183–184, pl. 10, fig. 25, 25a; 1844g: 154; 1844z3: [3]; 1847z5: pl. 15, fig. 9; 1849z3: 88–89. Palermo & Scordia, Sicily, Italy; fossil. Syntypes, PHB MB Ga. 452 (V) 53 (n = 7). Synonym of *Clelandella miliaris* (Brocchi, 1814), known from the Pleistocene to Recent (Fretter & Graham, 1977: 71–74, figs. 52, 53, listed under *Trochus clelandi* W. Wood, 1828, another junior synonym; Sabelli et al., 2009: 137).



- minor*, *Trochus* – Philippi, 1851e: 137–138; 1848k: pl. 23, fig. 15, ex Troschel ms. Locality unknown. This was noted as a manuscript name, the description being by Philippi. The uncaptioned plate (1848) appeared three years before the text (1851) making the name available. Synonym of *Phasianotrochus irisodontes* (Quoy & Gaimard, 1834), from southern Australia (Pilsbry, 1889a: 133; Cotton, 1959: 108–110, fig. 51).
- morum*, *Trochus* (*Clanculus* – as “*Clanculas*”) – Philippi, 1849h: 109; 1849z3: pl. 39, fig. 5; 1855c: 265. Locality unknown. *Trochus morum* Philippi, 1849 (Pilsbry, 1889a: 55–56, pl. 14, figs. 31–32), or synonym of *Clanculus limbatus* (Quoy & Gaimard, 1834), from Australia (Cotton, 1959: 129–130, fig. 66).
- multigranus*, *Trochus* (*Clanculus*) – Philippi, 1849h: 127; 1849z3: pl. 36, fig. 6; 1852d: 239. Mediterranean. Synonym of *Clanculus coralinus* (Gmelin, 1791) (Priolo, 1953a: 93–95 [91–93]; Sabelli et al., 1990: 127).
- mutabilis*, *Trochus* – Philippi, 1851e: 166; 1849z3: pl. 26, figs. 18–22. Mediterranean. The uncaptioned plate (1849) appeared two years before the text (1851) making the name available. *Monodonta* (*Osilinus*) *mutabilis* (Philippi, 1851) (Priolo, 1953a: 92–93 [90–91], pl. 4, fig. 9; Cesari, 1987; Sabelli et al., 1990: 135, both as “1846”), or *Osilinus mutabilis* (Philippi, 1851) (Cesari & Pranovi, 1989 & 1990, as “1846”). Nordsieck (1974: 21) stated that this species was a junior synonym of *Trochus sitis* Récluz, 1843, but “we conserve, however, the well known name of *mutabilis* ....” Gofas & Jabaud (1997) discussed the status of this species and referred it to *Phorcus* Cossmann, 1888. Type species (OD) of *Mutilastra* F. Nordsieck, 1974, presumably a synonym of *Phorcus*.
- nebulosus*, *Trochus* (*Phorcus*) – Philippi, 1849h: 109–110; 1849z3: pl. 35, fig. 5; 1851e: 232; 1852d: 233. Alexandriam, Red Sea; Hemprich & Ehrenberg. Synonym of *Gibbula* (*Tumulus*) *umbilicaris* (Linnaeus, 1758) (Sabelli et al., 1990: 134).
- neritoides*, *Trochus* – Philippi, 1850a: 170; 1850q: pl. 44, fig. 4; 1855c: 303–304. Locality unknown; Hanley coll. The western Pacific *Monodonta* (*Neomonodonta*) *neritoides* (Philippi, 1850) (Higo et al., 1999: 58; Okutani, 2000: 66–67, fig. 67; Qi, 2004: 23, pl. 9O, as “1849”). Type species (OD) of *Neomonodonta* Kuroda & Habe, 1971.
- nitidissimus*, *Trochus* – Philippi, 1845z: 449 [*nomen nudum*]; 1847-l: 61, pl. 9, fig. 8. Westeregeln & Osterweddingen, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene; Halisches Museum. Possible senior synonym of *Tiburnus margaritula* (Sandberger, 1859) (Anderson, 1959: 55–57, pl. 2, fig. 4).
- nitidulus*, *Trochus* – Philippi, 1850a: 171; 1850q: pl. 44, fig. 9; 1855c: 306–307. Locality unknown; Hanley coll. Synonym of the Indo-Pacific *Phasianotrochus irisodontes* (Quoy & Gaimard, 1834) (Cotton, 1959: 108–110, fig. 51).
- nucleus*, *Trochus* – Philippi, 1850a: 171; 1850q: pl. 43, fig. 15; 1855c: 298. Locality Unknown [Indo-Pacific]; Hanley coll. *Rossiteria nuclea* (Philippi, 1850) (Higo et al., 1999: 68; Okutani, 2000: 80–81, fig. 133; Wilson, 1993: 94, as “1849”). Type species (M) of *Solanderia* P. Fischer, 1879, *non* Duchassaing & Michelin, 1846 [Cnidaria]. *Rossiteria* Brazier, 1895, *nom. nov. pro Solanderia* P. Fischer.
- obtusatus*, *Trochus* – Philippi, 1847z5: 30–31; 1846z3: pl. 6, figs. 7, 8. The uncaptioned plate (1846) appeared one year before the text (1847) making the name available. Locality not stated.
- occultus*, *Trochus* – Philippi, 1845n: 17 [29], pl. 6 [in text as “7”], fig. 8; 1845r: 39 [35], figure 8 actually *Trochus clanculoides* W. Wood, 1828; 1849z3: pl. 25, fig. 8; 1851e: 156. Locality unknown. His later treatments (1849z3, 1851e) make no mention of a wrong original figure, which was cited and reprinted. Synonym of the western Atlantic *Tegula fasciata* (Born, 1778) (Abbott, 1958: 25).
- ochotensis*, *Trochus* – Philippi, 1851e: 221–222; 1849z3: pl. 34, fig. 1, ex Middendorff ms. Okhotsk Sea. The uncaptioned plate (1849) appeared two years before the text (1851) making the name available. Synonym of *Margarites schantaricus* (Middendorff, 1849) (Higo et al., 1999: 55, as “Middendorff in Philippi”; Kantor & Sysoev, 2005: 34–35).
- ochroleucus*, *Trochus* – Philippi, 1850a: 187; 1849z3: pl. 36, fig. 16; 1852d: 243–244. Locality unknown; Hanley coll. The uncaptioned plate (1849) appeared one year before the text (1850) making the name available. The Australian *Clanculus ochroleucus* (Philippi, 1850) (Cotton, 1959: 140–141, fig. 75; Wilson, 1993: 87, pl. 8, fig. 7; Wells et al., 2005: 298, both as “1853”).
- omphalium*, *Trochus* (*Phorcus*) – Philippi, 1849h: 110; 1849z3: pl. 39, fig. 16; 1855c: 270–271. Locality unknown. Syntypes, SMF 314006 (n = 4, “Panama”) (largest, 15.9 mm x 17.7 mm). Synonym of the eastern Pacific *Chlorostoma reticulatum* (W. Wood, 1828), *non* J. Sowerby, 1821, now known as *Tegula*



- verrucosa* McLean, 1970 (Keen, 1971: 342; Coan & Petit, 2011: 28). Either a petition to the ICZN would be required in order to continue using the McLean 1970 name, or Philippi's name should be used for this tropical eastern Pacific species.
- ottoi*, *Trochus* – Philippi, 1844g: 227, 303, pl. 28, fig. 9, 9a. Messina, Sicily, Italy; A. G. Otto; Pleistocene. The western Atlantic *Calliotropis ottoi* (Philippi, 1844) (Warén, 1991: 56, fig. 1B; Di Geronimo & La Perna, 1997: 396; Ibarrola et al., 2012: 63–64); type species (OD) of *Calliotropis* Seguenza, 1903.
- ovallei*, *Trochus* – Philippi, 1887a: 99 [1887b: 94], pl. 12, fig. 4. “Tumbez”, Chile; Cretaceous. Holotype, SGO.PI.807. *Tegula ovallei* (Philippi, 1887), Maastrichtian (Bandel & Stinnesbeck, 2000: 761, pl. 1, fig. b).
- oxytropis*, *Trochus* (*Euchele*) – Philippi, 1849h: 111; 1849z3: pl. 39, fig. 1; 1855c: 262. Locality unknown. Synonym of *Euchelus tricarinata* (Lamarck, 1822), from the Indian Ocean (Pilsbry, 1890a: 431, pl. 37, figs. 14–15).
- panamensis*, *Trochus* (*Polydonta*) – Philippi, 1849h: 127; 1850q: pl. 44, fig. 16; 1855c: 311–312. Panama; E. B. Philippi. The Panamic *Tegula* (*Agathistoma*) *panamensis* (Philippi, 1849) (Keen, 1971: 340–241, fig. 107; Ramírez et al., 2003: 258).
- parvula*, *Rotella* – Philippi, 1851c: 94. Locality unknown; Anton.
- parvulus*, *Globulus* – Philippi, 1853d: 48–49, pl. 7, figs. 11, 12, ex Anton ms. Locality unknown. The species name was indicated as being “in litt.”, so Philippi is regarded as being its author. Synonym of the Indo-Pacific *Umbonium vestiarium* (Linnaeus, 1758) (Pilsbry, 1890a: 451).
- parvulus*, *Trochus* – Philippi, 1844g: 155, 302, pl. 25, fig. 11. Pezzo, near Rhegium, Calabria, Italy; fossil. Synonym of *Jujubinus montagui* (W. Wood, 1828), Pleistocene to Recent (Sabelli et al., 1990: 136).
- parvus*, *Trochus* – Philippi, 1851e: 175; 1849z3: pl. 27, fig. 15, ex Troschel ms., *non* da Costa 1778, *non* J. Adams, 1797. Locality unknown. The uncaptioned plate (1849) appeared two years before the text (1851) making the name available. The name is indicated as having been taken from a museum label, although Troschel was credited as being its author. Synonym of the Indo-Pacific *Monodonta canaliferus* (Lamarck, 1822) (Pilsbry, 1889a: 88–89, pl. 34, fig. 27).
- patricius*, *Trochus* – Philippi, 1851b: 41–42; 1851e: pl. 46, fig. 11; 1855c: 326–327, attributed to Gruner. Locality unknown; Gruner coll. Syntype, ZMB 29927 (16.0 mm x 18.7 mm).
- Monilea patricus* (Philippi, 1851) (Pilsbry, 1890a: 248–249, pl. 41, figs. 30–31). Pilsbry listed the locality as “Central American coasts (?)” but noted that his presumed locality was “very doubtful”.
- pennanti*, *Trochus* – Philippi, 1851e: 224–225; 1849z3: pl. 34, fig. 10. England; Hanley. The uncaptioned plate (1849) appeared two years before the text (1851) making the name available. Holotype, NHMUK 1909.5.17.3 (“English Coast”) (13.8 mm x 15.2 mm). *Gibbula* (*Steromphala*) *pennanti* (Philippi, 1851) (Tomlin, 1921; Peile, 1922; Fretter & Graham, 1977: 54–55, figs. 37, 38, as “1836”; Sabelli et al., 1990: 133, as “1846”).
- perdix*, *Trochus* – Philippi, 1851e: 150; 1848k: pl. 24, fig. 17, ex Koch ms. Locality unknown. The uncaptioned plate (1848) appeared three years before the text (1851) making the name available. The name was specifically indicated as being “in literis”. Synonym of *Monodonta sagittifera* (Lamarck, 1822), from South Africa (Pilsbry, 1889a: 115, pl. 24, fig. 91), although Pilsbry's synonymy is probably in error (Herbert, 2015: 57, fig. 7-J).
- peronii*, *Trochus* – Philippi, 1850q: 135–136; 1848k: pl. 23, fig. 9. Australia. The uncaptioned plate (1848) appeared two years before the text (1850) making the name available. *Cantharidus peronii* (Philippi, 1850) (Pilsbry, 1889a: 132, pl. 34, figs. 12–14), or a variety of the Australian *Phasianotrochus eximius* (Perry, 1811) (Cotton, 1959: 105–106, fig. 48).
- personatus*, *Trochus* – Philippi, 1849z3: 78; 1847z5: pl. 14, fig. 7, *nom. nov. pro Monodonta ringens* Philippi, 1846i, *non* Menke, 1843. Australia. The uncaptioned plate (1847) appeared two years before the text (1849) making the name available. The Australian *Clanculus personatus* (Philippi, 1849) (Cotton, 1959: 129, fig. 65; Wilson, 1993: 88, pl. 8, fig. 12a, b; Wells et al., 2005: 298, all as “1846”).
- pfeifferi*, *Trochus* – Philippi, 1846i: 104; 1849z3: pl. 25, fig. 2; 1851e: 152–153. Locality unknown; Pfeiffer. The Japanese *Omphalius pfeifferi* (Philippi, 1846) (Higo et al., 1999: 51; Okutani, 2000: 54–55, fig. 5).
- pictus*, *Trochus* – Philippi, 1846i: 104, *non* W. Wood, 1828. Locality unknown. Synonym of *Gibbula* (*Colliculus*) *nivosa* A. Adams, 1851 (Sabelli et al., 1990: 131). See also above under: *alveolatus*, *Trochus* – Philippi, 1851e.
- piperinus*, *Trochus* (*Diloma*) – Philippi, 1849h: 111; 1849z3: pl. 30, fig. 10; 1851e: 204–205.



- Hawaii "?". The Japanese *Diloma* (*Diloma*) *piperinus* (Philippi, 1849) (Higo et al., 1999: 58; Okutani, 2000: 66–67, fig. 65).
- pisum*, *Trochus* – Philippi, 1849h: 111–112; 1849z3: pl. 30, fig. 11; 1851e: 205–206. Antilles; Gruner. *Gibbula pisum* (Philippi, 1849) (Pilsbry, 1890a: 241–242, pl. 31, figs. 38–40).
- plebejus*, *Trochus* – Philippi, 1851b: 41; 1851e: pl. 46, fig. 10; 1855c: 326. Locality unknown; Ettmüller coll. The southeast Australian *Clanculus plebejus* (Philippi, 1851) (Cotton, 1959: 138–139, fig. 73; Wilson, 1993: 88; Wells et al., 2005: 298). South Australian type species (OD) of *Mesoclanculus* Iredale, 1924. Beu (2010b: 72) placed this genus as a junior synonym of *Clanculus* Montfort, 1810. Sporadic records from New Zealand are probably the result of rafting, not larval dispersal (Beu, 2010b: 72–75).
- poepigii*, *Trochus* – Philippi, 1887a: 102 [1887b: 96], pl. 11, fig. 20. Navidad & Matanzas, Chile; Tertiary [Miocene]. Lectotype, SGO.PI.815 (figured specimen, from Matanzas), selected by Nielsen et al. (2004: 80, in plate caption); paralectotype, SGO.PI.811 (Navidad). *Gibbula poepigii* (Philippi, 1887) (Nielsen et al., 2004: 81, figs. 37–39).
- polaris*, *Trochus* – Philippi, 1852d: 249–250; 1849z3: pl. 37, fig. 9, ex Beck ms. Iceland & Spitzbergen; Kröyer. The uncaptioned plate (1849) appeared three years before the text (1852) making the name available. Listed by Macpherson (1971: 16) and by Kantor & Sysoev (2005: 35) as “1846”. Synonym of *Margarites striatus* (Leach, 1819) (Kantor & Sysoev (2005: 35).
- porcatus*, *Trochus* – Philippi, 1850a: 187–188. Locality unknown; Hanley coll. *Cantharidus porcatus* (Philippi, 1850) (Pilsbry, 1889a: 136–137, pl. 34, fig. 31).
- preissianus*, *Trochus* (*Phorcus*) – Philippi, 1849h: 123; 1849z3: pl. 28, fig. 3; 1851e: 177. Australia; Preiss. *Notogibbula preissiana* (Philippi, 1849) (Cotton, 1959: 170–171, fig. 100; Wilson, 1993: 79, pl. 9, fig. 7; Wells et al., 2005: 299, all as “1848”).
- puella*, *Trochus* – Philippi, 1851b: 41; 1851e: pl. 46, fig. 12; 1855c: 327–328. Locality unknown; Gruner coll. Synonym of *Cantharidus pulcherrimus* (W. Wood, 1828), from Australia (Pilsbry, 1889a: 126), or as *Prothalotia pulcherrima* (W. Wood, 1828) (Cotton, 1959: 121–122, fig. 60).
- pumilio*, *Trochus* – Philippi, 1844g: 226, 303, pl. 28, fig. 7, 7a, 7b; 1847z5: pl. 15, fig. 19; 1849z3: 94. “Trochorum”, Italy. Synonym of *Jujubinus striatus* (Linnaeus, 1758) (Sabelli et al., 1990: 137).
- punicea*, *Monodonta* – Philippi, 1846i: 100; 1847z5: pl. 14, fig. 2; 1849z3: 73–74, as *Trochus puniceus*. New Zealand “?”. Herbert (1993a: 261–268) “emended” the type locality from “New Zealand” to Durban, South Africa, because the species is only found from the eastern coast of Africa and the offshore islands. The east African *Clanculus puniceus* (Philippi, 1846) (Herbert, 2015: 65).
- pustulosus*, *Trochus* (*Polydonta*) – Philippi, 1850a: 188–189; 1850q: pl. 44, fig. 6; 1855c: 305. Locality unknown; Hanley coll. Pilsbry (1889a: 30) listed this in the synonymy of *T. calcaratus* Souverbie, 1875 (New Caledonia), which would, of course, be a junior synonym of Philippi’s name.
- pygmaeus*, *Trochus* – Philippi, 1844g: 153–154, 302, pl. 25, fig. 13; 1850q: pl. 42, fig. 7; 1855c: 287. Magnisi Peninsula, Sicily, Italy. *Trochus pygmaeus* Philippi, 1844 (Pilsbry, 1890a: 476, pl. 39, figs. 29–30).
- pyrgos*, *Trochus* – Philippi, 1850a: 189; 1850q: pl. 43, fig. 14; 1855c: 297–298. Australia; Hanley coll. Synonym of the Australian *Odonotrochus indistinctus* (W. Wood, 1828).
- quiriquinae*, *Trochus* – Philippi, 1887a: 100 [1887b: 94], pl. 11, fig. 22. Isla Quiriquina, Chile; Cretaceous. Holotype, SGO.PI.816. Synonym of *Solariella unio* (Philippi, 1887) (Wilckens, 1904: 194–195), or *Trochus* (*Lewisiella*) *quiriquinae* Philippi, 1887 (Wetzel, 1930: 64–65).
- quoyi*, *Trochus* – Philippi, 1851e: 139; 1848k: pl. 23, fig. 17. Australia. Replacement name for *Trochus australis* Quoy & Gaimard, 1834 (p. 248), *non* Broderip, 1832. Syntype, MNHN Paris (n = 1, 18.8 mm x 9.7 mm) (of *T. australis* Quoy & Gaimard). Synonym of the Indo-Pacific *Phasianotrochus eximius* (Perry, 1811) (Pilsbry, 1889a: 131–132, as *P. badius* (W. Wood, 1828); Cotton, 1959: 105–106, fig. 48); concerning the latter two names: Coan & Petit, 2011: 25–26.
- radula*, *Trochus* (*Diloma*) – Philippi, 1849h: 124; 1849z3: pl. 30, fig. 9; 1855c: 204, ex Parreyss ms. Hawaii “?” (1849h); unknown (1855c). Philippi’s two accounts make clear that he only received a labeled specimen from Parreyss and that he alone is responsible for its description. The Japanese *Diloma* (*Diloma*) *radula* (Philippi, 1849) (Higo et al., 1999: 59; Okutani, 2000: 66–67, fig. 66).
- rigatus*, *Trochus* (*Phorcus*) – Philippi, 1849h: 124–125; 1849z3: pl. 28, fig. 14; pl. 39, fig. 8, var.; 1851e: 184–185; 1855c: 267, var.



- Adelaide, Australia. *Monilea rigata* (Philippi, 1849) (Pilsbry, 1890a: 251, pl. 41, figs. 32–33), or synonym of *Notogibbula lehmanni* (Menke, 1843) (Cotton, 1959: 171–172, fig. 101).
- ringens*, *Monodonta* – Philippi, 1846i: 99–100, *non* Menke, 1843. Locality unknown; Pfeiffer & Gruner colls. Renamed as *Trochus personatus* Philippi, 1849z3 (q.v.).
- roseus*, *Turbo* – Philippi, 1850p: 85–86; 1849z2: pl. 19, fig. 10. Mediterranean. The uncaptioned plate (1849) appeared one year before the text (1850) making the name available. Synonym of *Leptothyra cicer* (Menke, 1844), from South Africa (Pilsbry in Tryon & Pilsbry, 1889a: 254, pl. 54, fig. 62), now *Gibbula cicer* (Menke, 1844) (Kilburn & Rippey, 1982: 40).
- rossii*, *Trochus* – Philippi, 1855c: 288; 1850q: pl. 42, fig. 9. Locality unknown. The uncaptioned plate (1850) appeared five years before the text (1855) making the name available. Synonym of *Margarites groenlandicus* (Gmelin, 1791), northern Atlantic (Kantor & Sysoev, 2005: 33–34).
- rotellaeformis*, *Trochus* – Philippi, 1850a: 189–190; 1850q: pl. 44, fig. 2; 1855c: 302. Locality unknown; Hanley coll. Pilsbry (1890a: 262) listed this in the synonymy of *Monilea rhodomphala* (Souverbie, 1875), from New Caledonia, while noting that Philippi's "name of course has priority."
- rubescens*, *Trochus* – Philippi, 1836a: 182–183. Licata, Sicily, Italy; Schott.
- rubricatus*, *Trochus* (*Polydonta*) – Philippi, 1849h: 125; 1849z3: pl. 31, fig. 13; 1851e: 213. Locality unknown. *Trochus rubricatus* Philippi, 1849, from Japan (Pilsbry, 1889a: 32–33, pl. 7, figs. 70–71).
- sacellum*, *Trochus* – Philippi, 1855c: 309; 1850q: pl. 44, fig. 13. Locality unknown; Gruner coll. The uncaptioned plate (1850) appeared five years before the text (1855) making the name available. The western Pacific *Trochus* (*Trochus*) *sacellum* Philippi, 1855 (Higo et al., 1999: 56).
- saga*, *Trochus* – Philippi, 1846i: 103; 1847z5: pl. 16, fig. 6; 1849z3: 99. Locality unknown; Stuttgart coll. *Trochus saga* Philippi, 1846 (Pilsbry, 1889a: 41, pl. 14, figs. 14–15).
- scabriculus*, *Trochus* (*Phorcus*) – Philippi, 1849h: 125, ex Busch ms. Antilles, *non* Monterosato, 1883. This species was indicated as a Busch ms species and thus Philippi is regarded as its author. *Chlorostoma scabriculus* (Philippi, 1849) (Pilsbry, 1889a: 192, pl. 61, figs. 16–18).
- scabrosus*, *Trochus* – Philippi, 1850a: 190–191; 1850q: pl. 43, fig. 3; 1855c: 292. Locality unknown; Bellanger & Hanley collection. Type species (M) of *Belangeria* P. Fischer, 1879. The Arabian Gulf *Trochus* (*Belangeria*) *scabrosus* Philippi, 1850 (Bosch et al., 1995: 34, fig. 37).
- scalaris*, *Trochus* – Philippi, 1844c: 140 [18], pl. 4, fig. 11, ex Anton ms, *non* Romer, 1836. Laguayra [La Guaira, Venezuela], ex Koch. Synonym of *Tegula lividomaculata* (C. B. Adams, 1845) (Abbott, 1958: 26–27; 1974: 50).
- schrayeri*, *Trochus* – Philippi, 1850q: 131–132; 1848k: pl. 23, fig. 3, ex Troschel ms, as *T. schayeri*. Tasmania; Schroyer. This species was specifically noted as a manuscript name, the description being by Philippi. It was also noted in two places as having been obtained from a "von Schroyer", so the header "*schayeri*" must have been a lapsus. The uncaptioned plate (1848) appeared two years before the text (1850) making the name available. Synonym of *Phasianotrochus irisodontes* (Quoy & Gaimard, 1834) (Cotton, 1959: 108–110, fig. 51).
- sculptus*, *Trochus* – Philippi, 1846z3: 14–15, pl. 3, figs. 8, 9. West Indies. A senior homonym of *T. sculptus* Binkhorst, 1861 (Cretaceous, Belgium).
- seminulum*, *Trochus* – Philippi, 1855c: 308–309; 1850q: pl. 44, fig. 12. Locality unknown. The uncaptioned plate (1850) appeared five years before the text (1855) making the name available. *Gibbula seminum* (Philippi, 1855) (Pilsbry, 1890a: 222, pl. 33, fig. 85).
- senatorius*, *Trochus* – Philippi, 1851b: 44; 1851e: pl. 46, fig. 7; 1855c: 324–325. Locality unknown. Synonym of *Tectus conus* (Gmelin, 1791), Indo-Pacific (Hidalgo, 1905: 85, as a junior synonym of *Trochus acutangulus* "Chemnitz").
- servilis*, *Trochus* – Philippi, 1851b: 40; 1851e: pl. 46, fig. 14; 1855c: 329. Locality unknown; Etmüller coll.
- solandri*, *Trochus* – Philippi, 1851e: 180–181; 1849z3: pl. 28, fig. 8, *nom. nov. pro Monodonta crenulata* Menke, 1843, *non Trochus crenatulus* Brocchi, 1814. Western Australia. The uncaptioned plate (1849) appeared two years before the text (1851) making the name available. Type material would be Menke's specimen(s). The Indian Ocean *Monilea solandri* (Philippi, 1851) (Tan & Woo, 2010: 14), generally in the literature as *M. solanderi*, presumably on the assumption it was named for Daniel Solander, but there is no internal



- evidence for that, and the shorter spelling is in both Philippi's text and in his index.
- sordidus*, *Trochus* – Philippi, 1850a: 191; 1850q: pl. 44, fig. 1; 1855c: 298. Locality unknown; Hanley coll. *Chlorostoma sordidus* (Philippi, 1850) (Pilsbry, 1889a: 188, pl. 61, figs. 7–8).
- spadiceus*, *Trochus* (*Clanculus*) – Philippi, 1849h: 110; 1849z3: pl. 36, fig. 7; 1852d: 239. Locality unknown. Neotype, ZMB 104023 (Espirinha, São Tomé) (13.5 mm x 15.1 mm), designated by Rubio & Rolán (2002: 57, figs. 143–144). *Clanculus spadiceus* (Philippi, 1849).
- spinula*, *Trochus* – Philippi, 1887a: 100 [1887b: 95], pl. 11, fig. 25. Isla Quiriquina, Chile; Cretaceous. Holotype, SGO.PI.806. Wilckens (1904: 195) thought that this was a doubtful species, possibly a fragment of *Fusus difficilis* d'Orbigny, 1835 (Buccinidae).
- steinmanni*, *Trochus* – Philippi, 1887a: 100 [1887b: 95], pl. 11, fig. 26. Isla Quiriquina, Chile; Cretaceous. Holotype, SGO.PI.819. Synonym of *Solariella unio* (Philippi, 1887) (Wilckens, 1904: 194–195; Wetzel, 1930: 65).
- straminea*, *Trochus magus* var. – Philippi, 1836a: 180, as var. “totam stramineam.” Locality presumably Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1885: 375), as *Trochus magus* var. *straminea* Philippi, 1836. Synonym of *Gibbula magus* (Linnaeus, 1758) (Priolo, 1951b: 266 [58]).
- suavis*, *Trochus* – Philippi, 1850a: 191–192; 1850q: pl. 43, fig. 1; 1855c: 301–302. Locality unknown; Hanley coll. Syntype, NHMUK 1909.5.17.5 (“Japan”, ex Hanley) (12.2 mm x 13.1 mm). The Indo-Pacific *Diloma* (*Pictodiloma*) *suavis* (Philippi, 1850) (Higo et al., 1999: 59, as “1849”; Okutani, 2000: 66–67, fig. 64; Poppe & Tagaro, 2011c: 634–635, pl. 1308, fig. 3, as “1849”). Type species (M) of *Pictodiloma* Habe, 1946.
- subviridis*, *Trochus* (*Polydonta*) – Philippi, 1849h: 126; 1949z: pl. 38, fig. 7; 1855c: 259. Locality unknown. Herbert (1993a: 284, 290) noted that Pilsbry (1889: 39) had erroneously listed Philippi's species as a synonym of *T. nigropunctatus* Reeve, 1861, which led to subsequent authors using Reeve's name for the common South African species. Herbert (1993a: 290) concluded that “Without examining the type material of *T. subviridis*, if this is still extant (none in ZMHB, personal observation), it is impossible to make a decisive comment on this and I prefer to maintain the long established and widely used name” *Trochus* (*T.*) *nigropunctatus* Reeve, 1861.
- suturalis*, *Delphinula* – Philippi, 1844z4: 55, [87], pl. 3, fig. 34. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. Syntype, PHB MB Ga. 460 (V) 43 (8.3 mm x 9.3 mm). *Solariella* (*Solariella*) *suturalis* (Philippi, 1844) (Anderson, 1959: 47–49, pl. 4, figs. 1a–b; Janssen, 1978a: 27–28, 1978b: 146–147, pl. 9, fig. 13).
- suturalis*, *Trochus* – Philippi, 1836a: xii, 185, pl. 10, fig. 23, 23a; 1844g: 156. Sciacca, Sicily, Italy; fossil. *Callumbonella suturalis* (Philippi, 1836), a deep-water species from northwest Africa and the western Mediterranean (Malaquias et al., 2003; Landau et al., 2003: 69, pl. 18, figs. 2–3; Sabelli et al., 1990: 136; Nolf & Verstraeten, 2013). Rolán et al. (2009: 645) added that “We also have some doubts about [Philippi's] fossil species being considered the same as the Recent ones,” so that “if the fossil and the Recent species are conchologically different, the name to be employed [for the Recent species] would be *Callumbonella folini* (P. Fischer, 1883).” However, Nolf & Verstraeten (2013: 3, 7) concluded that *C. folini* was merely “a large form from the Mediterranean” of Philippi's species.
- tener*, *Trochus* – Philippi, 1851e: 141–142; 1848k: pl. 24, fig. 2, ex Troschel ms. Locality unknown. Troschel supplied the name and was noted as having prepared the figure, but the description appears to be by Philippi. The uncaptioned plate (1848) appeared three years before the text (1851) making the name available. (For the following species in his text, *Trochus morio* Troschel, in Philippi – p. 142 – Troschel is acknowledged both for the figure and the description.) *Monodonta tener* (Philippi, 1851) (Pilsbry, 1889a: 116, pl. 35, figs. 17, 18).
- torulosus*, *Trochus* – Philippi, 1843h: 69 [9], pl. 2, fig. 12. Locality unknown. Dall (1909: 291) recorded this from Peru, as a junior synonym of *T. quadricostatus* W. Wood, 1828, which Dall attributed to “Gray”. Concerning the latter: DeVries, 2007; W. Wood's species is type of the genus *Cantallocostoma* DeVries, 2007.
- tridens*, *Trochus* – Philippi, 1844p: 139–140 [17–18], pl. 4, fig. 10, ex Menke ms. Peru. *Chlorostoma tridens* (Philippi, 1844) (Pilsbry, 1889a: 175).
- troschelii*, *Trochus* – Philippi, 1850q: 130; 1848k: pl. 23, fig. 2. South Africa; Viet. The uncaptioned plate (1848) appeared two years



before the text (1850) making the name available. In describing this species, Philippi noted that it had been labeled in the museum in Berlin [i.e., ZMB] as *Trochus punctatus*, but that this name had already been used for another species. In fact, *Trochus punctatus* was a *nomen nudum* in Krauss (1848: 98). Synonym of *Thalotia conica* (Gray 1827), from South Australia (Cotton, 1959: 116; Herbert, 1993a: 246, who noted that this species was “erroneously localized to South Africa”).

*turdus*, *Trochus* – Philippi, 1855c: 308; 1850q: pl. 44, fig. 11. Locality unknown. The uncaptioned plate (1850) appeared five years before the text (1855) making the name available. *Gibbula turdus* (Philippi, 1855) (Pilsbry, 1890a: 209–210, pl. 33, figs. 98–99).

*turris*, *Trochus* – Philippi, 1846i: 102, *non* Pusch, 1837. Locality unknown. Renamed *Trochus altus* Philippi, 1851e, q.v.

*unidentatus*, *Trochus* – Philippi, 1844g: 150, 302, pl. 25, fig. 8; 1847z5: pl. 15, fig. 13; 1849z3: 91. Sicily, Italy. *Jujubinus unidentatus* (Philippi, 1844) (Sabelli et al., 1990: 137). Type species (M) of *Manotrochus* P. Fischer, 1885, a synonym of *Jujubinus* Monterosato, 1884.

*unio*, *Trochus* – Philippi, 1887a: 100 [1887b: 94–95], pl. 11, fig. 23. “Tumbez”, Chile; Ovalle; Cretaceous. *Solariella unio* (Philippi, 1887) (Wilckens, 1904: 194–195; Wetzel, 1930: 65).

*urvillei*, *Trochus* – Philippi, 1851e: 215–216; 1849z3: pl. 32, fig. 4. Australia. The uncaptioned plate (1849) appeared two years before the text (1851) making the name available. Species name based on a specimen of *Trochus fimbriatus* figured in Quoy & Gaimard (1834: 229, pl. 61, fig. 9). Holotype, MNHN Paris (specimen cracked).

*ustus*, *Trochus* (*Phorcus*) – Philippi, 1849h: 101; 1850q: pl. 41, fig. 3; 1855c: 278–279. Locality unknown.

*variolosus*, *Trochus* – Philippi, 1855c: 308–309; 1850q: pl. 44, fig. 12, *nom. nov. pro Trochus tornatus* Jonas, in Philippi, 1850a: 16, *non* Philipps, 1829 [also *non* Röding, 1798, and *non* Gravenhorst, 1807]. Pacific Ocean; Hamburg Museum. The uncaptioned plate (1850) appeared five years before the text (1855) making the substitute name available.

*veneficus*, *Trochus* – Philippi, 1887a: 101 [1887b: 95], pl. 12, fig. 8. Navidad, Chile; Tertiary [Miocene]. Lectotype, SGO.PI.817 (selected by Nielsen et al., 2004: 82, figs. 43–45); paralectotypes SGO.PI.4681, 4682;

*Fagnastesia veneficus* (Philippi, 1887); type species (OD) of *Fagnastesia* Nielsen et al., 2004.

*venustulus*, *Trochus* (*Margarita*) – Philippi, 1858b: 23. Islas Chonos, Chile; Fr. Fonk.

*villana*, *Monodonta* – Philippi, 1846i: 101; 1847z5: pl. 14, fig. 3; 1849z3: 74, as *Trochus villanus*. Guinea. Neotype, ZMB 104021 (Takoradi, Ghana) (20.0 mm x 19.3 mm), designated by Rubio & Rolán (2002: 62, figs. 105, 107, 109, 145–146). However, SMF 314185 is original type material (21.5 mm x 22.3 mm); overlooked by Rubio & Rolán (2002). The west African *Clanculus villanus* (Philippi, 1846).

*villicus*, *Trochus* – Philippi, 1844g: 152, 302, pl. 25, fig. 14; 1849z3: pl. 29, fig. 17; 1851e: 194. Sicily, Italy. Syntypes, SMF 314075 (n = 3); ZMB 12174 (n = 4, largest, 8.1 mm x 9.8 mm). Synonym of *Gibbula* (*Phorcus*) *philiberti* (Récluz, 1843) (Priolo, 1951b: 274–275 [66–67]; Sabelli et al., 1990: 132).

*virgulatus*, *Trochus* – Philippi, 1850q: 136; 1851e: 137; 1848k: pl. 23, fig. 9. Australia. The uncaptioned plate (1848) appeared two years before the text (1850) making the name available; the second part of the description was published in 1851 (due to a page break). Synonym of *Phasianotrochus irisodontes* (Quoy & Gaimard, 1834).

*vulneratus*, *Trochus* – Philippi, 1850a: 16; 1850q: pl. 44, fig. 7; 1855c: 305–306. Locality unknown; Hanley coll. *Gibbula vulneratus* (Philippi, 1850) (Pilsbry, 1890a: 241, pl. 51, figs. 10–11).

*zebrinus*, *Trochus* – Philippi, 1846i: 105; 1849z3: pl. 26, fig. 6; 1851e: 161–162. Locality unknown (1846i); Tasmania (1851e). *Monodonta striolata* (Quoy & Gaimard, 1834) (Pilsbry, 1889a: 99).

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“*Clanculas*” – Philippi, 1849h: 109. Error *pro Clanculus* Montfort, 1810.

“*acutangulus*, *Trochus*” – Philippi, 1848k: 36–37. Listed by Sherborn (1922: 59) as by Philippi, this name based on a Chemnitz figure was actually first made available by Anton (1838).

“*aethiops*, *Trochus*” – Philippi, 1851e: 147–148. Philippi credited himself with this name in the header, but this represented the transfer of *Turbo aethiops* Gmelin, 1791, to *Trochus*.

“*articulatus*, *Trochus*” – Philippi, 1836a: xii, 177. As “*mihi*” for a transfer of *Monodonta articulata* Lamarck, 1822, to *Trochus*.



"*canaliculatus, Trochus*" – Philippi, 1836a: xii, 180. As "mihi" for a transfer of *Monodonta canaliculata* Lamarck, 1822, to *Trochus*.

"*crispus, Trochus*" – Philippi, 1836a: xii, 183, ex König ms. Indicated by Philippi as a Bronn manuscript name, it was actually made available by König (1825).

"*fragarioides, Trochus*" – Philippi, 1836a: xii, 177. As "mihi" on p. xii for a transfer of *Monodonta fragarioides* Lamarck, 1822, to *Trochus*.

"*gibberosus, Trochus*" – Philippi, 1846z3: 6 (attributed to Chemnitz). This name was attributed to Philippi by Sherborn (1926: 2678), but it was first made available by Dillwyn (1817).

"*iriodon, Trochus*" – Philippi, 1845r: 39. Invalid emendation of *Trochus irisodontes* Quoy & Gaimard, 1834.

"*jussieui, Monodonta*" – Philippi, 1836a: xii, 186. Credited by Sherborn (1927: 3303) to "Payraudeau in Philippi", this species had been made available by Payraudeau (1826: 136–137), as "*Monodonta jussioei*", in honor of Adrien de Jussieu.

"*lepidus, Trochus*" – Koch in Philippi, 1849z3: 84; 1847z5: pl. 15, fig. 4, *non* de Koninck, 1843. The uncaptioned plate (1847) appeared two years before the text (1849) making the name available. This species, which is a junior primary homonym, was credited by both Wilson (1993: 81) and Hickman (2005: 202–203) as being a Philippi species (but as "1846"). However, it was credited in the text as being by Koch, and it is more likely that Koch prepared the description.

"*lupines, Trochus*" – Cotton (1959: 142) attributed this to "Philippi, 1846" but it was first described by Menke, 1843.

"*multipes, Trochus*" – Philippi, 1850a: 169–170; 1851e: pl. 46, fig. 2; 1855c: 320–321. Keen (1971: 356) attributed this species to Philippi, but Philippi credited it to Jonas, and under our interpretation of the *Zeitschrift für Malakozoologie*, Jonas should be given credit for its authorship.

"*richardi, Trochus*" – Philippi, 1836a: xii, 181. As "mihi" for a transfer of *Monodonta richardi* Payraudeau, 1826, to *Trochus*.

"*tessellatus, Trochus*" – Pilsbry (1889a: 202) attributed this name to "Philippi, Conchyl. Cab., p. 190, t. 29, f. 9–12", but it was first described by Gmelin (1791).

"*tigrinus, Trochus*" – Philippi, 1847: 27. This species was listed by Sherborn (1931: 6520) as being a Philippi, ex Chemnitz name, but it was first made available by Anton (1838).

## Calliostomatidae

*adpersus, Trochus* – Philippi, 1851e: 217–218; 1849z3: pl. 34, fig. 8, ex Beck ms. Brazil [restricted to Praia do Leste, Ilha Guaíba, Rio de Janeiro, by Clench & Turner, 1960]. For *Trochus eximius* Reeve *sensu* Philippi, 1844, *non* Reeve 1843. The uncaptioned plate (1849) appeared two years before the text (1851) making the name available. *Calliostoma aspersum*, unjustified emendation by Lange de Morretes (1949: 58). *Calliostoma (Kombologion) adpersum* (Philippi, 1851) (Clench & Turner, 1960: 46–48, pls. 30, 31; Abbott & Dance, 1982: 38; Rios, 1994: 33, pl. 9, fig. 94). Type material presumed to be lost (Quinn, 1992: 107–108).

*aeruginosus, Trochus* – Philippi, 1850a: 146–147; 1850q: pl. 45, fig. 1; 1855c: 314. Locality unknown; Lischke coll. *Calliostoma aeruginosus* (Philippi, 1850) (Pilsbry, 1890a: 412–413, pl. 67, figs. 81–82).

*agrestis, Trochus* – Philippi, 1843d: 33 [3], pl. 1, fig. 6; 1847z5: pl. 13, fig. 13; 1848k: 67–68. Locality unknown. Synonym of the eastern Atlantic *Calliostoma zizyphinum* (Linnaeus, 1758) (Sabelli et al., 1990: 129).

*antonii, Trochus* – Philippi, 1843d: 32 [2], pl. 1, fig. 4; 1847z5: pl. 17, fig. 5; 1849z3: 105–106, ex Koch ms. Locality unknown. This species was originally credited to Koch in 1843 in the header, but the description was unsigned. In 1849, Philippi credited himself with this species, and we have followed this. *Calliostoma antonii* (Philippi, 1843), from Peru (Ramírez et al., 2003: 258).

*broderipi, Trochus* – Philippi, 1855c: 257–258; 1849z3: pl. 38, fig. 5. Australia. The uncaptioned plate (1849) appeared six years before the text (1855) making the name available. Synonym of *Calliostoma (Salsipotens) rubiginosum* (Valenciennes, 1846) (Cotton, 1959: 151–152, fig. 84; Wilson, 1993: 63, pl. 10, fig. 15).

*cecillei, Trochus* – Philippi, 1850a: 151–152; 1850q: pl. 43, fig. 2; 1855c: 291–292. Formosa, China; Cécille via Largilliert. *Calliostoma cecillei* (Philippi, 1850) (Pilsbry, 1890a: 342, pl. 67, fig. 64; Hidalgo, 1905: 91). Some sources have listed "*C. cecillei* Nomura & Hatai, 1935", as a junior synonym of *C. unicum* (Dunker, 1860), from Japan. In fact, Nomura & Hatai (1935: 43, pl. 2, figs. 5–6) expressly referred to Philippi's description, and Nomura (1935: 216, pl. 10, fig. 13) stated that: "The Japanese form hitherto known



- under the name of *C. unicum* (Dunker) certainly belongs to Philippi's species." At most, the use of "*cecillei*" for Japanese specimens would be a misidentification (not a new species), if Philippi's and Dunker's species are regarded as distinct.
- chemnitzii*, *Trochus* – Philippi, 1848k: 63–64; 1847z5: pl. 13, fig. 7, *non* Valenciennes, 1846. Portugal; Beck. The uncaptioned plate (1847) appeared one year before the text (1848) making the name available. Synonym of the eastern Atlantic *Calliostoma zizyphinum* (Linnaeus, 1758) (Sabelli et al., 1990: 129).
- comtus*, *Trochus* – Philippi, 1851b: 42; 1851e: pl. 46, fig. 6; 1855c: 324. Locality unknown; Largilliert coll. *Calliostoma comtum* (Philippi, 1851) (Pilsbry, 1890a: 354, pl. 18, fig. 24).
- dubius*, *Trochus* – Philippi, 1844g: 149–150, 302, pl. 25, fig. 7, as "*T. dubius* var. *levior*"; 1847z5: pl. 13, fig. 11a, b; 1848k: 66–67, *non* *T. dubius* Dillwyn, 1817, *non* T. Brown, 1843. Sicily, Italy. Synonym of *Calliostoma conulus* (Linnaeus, 1758) (Sabelli et al., 1990: 128), or *Calliostoma dubium* (Philippi, 1844) (Priolo, 1950: pl. 1, figs. 6–7, 1951a: 115–116 [47–48]; Giribet & Peñas, 1997: 47 [9]).
- elegantulus*, *Trochus* – Philippi, 1841f: 22, *non* W. Wood, 1828; 1844z4: 22, 55, [87], pl. 3, fig. 35. Tertiary near Wilhelmshöhe; [Late Oligocene]. Synonym of *Calliostoma serratocostatum* (Speyer, 1869) (Janssen, 1978b: 147–148, pl. 10, fig. 15); previously treated as a valid species of *Calliostoma* (Anderson, 1959: 51–52, pl. 2, figs. 7a–7c; Tembrock, 1962: 120; Janssen, 1978a: 27). Type material lost (R. Janssen, pers. comm., April 2013).
- ferruginosus*, *Trochus* – Philippi, 1850a: 154–155; 1850q: pl. 44, fig. 14; 1855c: 310. Locality unknown; Gruner coll. Probable syntype, ZMB 29934 (ex Gruner) (26.3 mm x 22.3 mm).
- fonki*, *Trochus* – Philippi, 1858b: 22; 1860a: 185–186 [1860b: 167]. Islas Chonos, Chile; Fr. Fonk. *Calliostoma fonki* (Philippi, 1858) (Dall, 1909: 240; Carcelles & Williamson, 1951: 264; Valdovinos, 1999: 126; Forcelli, 2000: 61; Cárdenas et al. (2008: 208), all as *C. "fonki"* and as "1860"; Letelier et al., 2003: 62, as "1845").
- fragum*, *Trochus* – Philippi, 1849h: 106; 1849z3: pl. 38, fig. 4; 1855c: 257. Locality unknown; Gruner. *Calliostoma fragum* (Philippi, 1849) (Pilsbry, 1890a: 348–349, pl. 18, figs. 13–14 (but "may be a *Thalotia*, allied to *T. pyrgus*"); Bosch et al., 1995: 33, fig. 33).
- fulvus*, *Trochus* (*Trochus*) – Philippi, 1849h: 106–107; 1849z3: pl. 31, fig. 3; 1851e: 209. Locality unknown. Synonym of *Calliostoma ornatum* (Lamarck, 1822), from Australia (Pilsbry, 1890a: 340).
- gualterianus*, *Trochus* – Philippi, 1848k: 69; 1847z5: pl. 11, fig. 15, *nom. nov. pro Trochus laevigatus* Philippi, 1836a, *non* Gmelin, 1791 (and two other uses of this name earlier than Philippi). Sicily, Mediterranean. The uncaptioned plate (1847) appeared one year before the text (1848) making the name available. Syntypes, SMF 314045 (n = 3, Sicily) (10.5 mm x 7.2 mm; 9.8 mm x 7.7 mm; 10.6 mm x 6.9 mm); ZMB 12096 (n = 9) (largest, 11.8 mm x 7.8 mm). The Mediterranean *Calliostoma gualterianum* (Philippi, 1848) (Priolo, 1951a: 117 [49]; Abbott & Dance, 1982: 36; Sabelli et al., 1990: 128; Landau et al., 2003: 55, pl. 12, fig. 3). Spelling corrected to *gualtierianus* (since it was named after N. Gualtieri), pursuant to ICZN Articles 31 and 32 by Salas & Luque (1986: 31–32).
- inconspicuus*, *Trochus* – Philippi, 1850a: 158; 1850q: pl. 43, fig. 16; 1855c: 310–311. Locality unknown; Hanley coll. *Calliostoma inconspicuum* (Philippi, 1850) (Pilsbry, 1890a: 343–344, pl. 18, fig. 18).
- laevigatus*, *Trochus* – Philippi, 1836a: xii, 175–176, pl. 11, fig. 2 [not cited in text]; 1844g: 150, 154, 302, pl. 25, fig. 31, var. "monstrosum, turritum", *non* Gmelin, 1791, *non* J. Sowerby, 1817, *non* Grateloup, 1832. Palermo, Sicily, Italy. Also fossil. Syntypes, SMF 314045 (n = 3, Sicily) (10.5 mm x 7.2 mm; 9.8 mm x 7.7 mm; 10.6 mm x 6.9 mm); ZMB 12096 (n = 9) (largest, 11.8 mm x 7.8 mm). Replacement name: *Trochus gualterianus* Philippi, 1848k (q.v.).
- levior*, *Trochus dubius* var. – Philippi, 1844g: 302, pl. 25, fig. 7 (name and figure only) Synonym of *Calliostoma dubium* (Philippi, 1844).
- lima*, *Trochus* – Philippi, 1850a: 159–160; 1850q: pl. 44, fig. 15; 1855c: 308–309. Locality unknown; Hanley coll. Syntype, NHMUK 1923.5.17.4 ("Panama", ex Hanley) (19.9 mm x 21.0 mm). *Calliostoma lima* (Philippi, 1850), from the eastern Pacific (Pilsbry, 1890a: 364–365, pl. 67, figs. 55–58), or as synonym of *Calliostoma antonii* (Koch in Philippi, 1843) (Keen, 1971: 332).
- meyeri*, *Trochus* – Philippi, 1849h: 100; 1850q: pl. 41, fig. 4; 1855c: 279–280. Locality unknown; A. B. Meyer. Synonym of the Australian *Calliostoma (Salsipotens) armillatum*



- (W. Wood, 1828) (Wilson, 1993: 63, pl. 10, fig. 21a, b).
- nobilis*, *Trochus* – Philippi, 1849z3: 86–87, pl. 38, fig. 1; 1847z5: pl. 15, fig. 6; 1855c: 255, “var.”, *non* Münster, 1835. West coast of Australia; Preiss. The uncaptioned plate (1847) appeared two years before the text (1849) making the name available. Synonym of *Calliostoma (Salsipotens) rubiginosum* (Valenciennes, 1846) (Cotton, 1959: 151–152, fig. 84; Wilson, 1993: 63, pl. 10, fig. 15).
- nocturnus*, *Trochus* – Philippi, 1849z3: 112–113; 1847z5: pl. 18, fig. 9. Locality unknown. The uncaptioned plate (1847) appeared two years before the text (1849) making the name available. *Calliostoma nocturnus* (Philippi, 1849) (Pilsbry, 1890a: 391, pl. 18, figs. 3–4, “probably synonymous” with *C. conulum* (Linnaeus, 1758), a Mediterranean species).
- nubilus*, *Trochus (Trochus)* – Philippi, 1849h: 110; 1849z3: pl. 38, fig. 2; 1855c: 255–256. Locality unknown. *Calliostoma nubilus* (Philippi, 1849) (Pilsbry, 1890a: 344, pl. 18, fig. 22, “very close to, or synonymous with, *C. jucundum* (Gould [1849])” from Brazil and Argentina). However, as Philippi’s 1849 paper was published in February, whereas Gould’s 1849 paper was published in March, Philippi’s name would have precedence over Gould’s if the two are regarded as synonyms.
- nudus*, *Trochus* – Philippi, 1845i: 65–66; 1847z5: pl. 15, fig. 10; 1849z3: 89. Strait of Magellan, Chile. Possible syntype, ZMB 114124 (ex Dunker) (8.8 mm x 7.8 mm). *Calliostoma nudum* (Philippi, 1845) (Carcelles & Williamson, 1951: 263; Castellanos & Landoni, 1989: 9–10, pl. 1, fig. 3; Valdovinos, 1999: 126; Forcelli, 2000: 60; Letelier et al., 2003: 61; Rosenfeld et al., 2015: 67–68, fig. 5A).
- pulchellus*, *Trochus* – Philippi, 1846i: 101–102; 1847z5: pl. 13, fig. 3; 1848k: 60–61. Locality unknown; Stuttgart coll. *Calliostoma pulchellum* (Philippi, 1846) (Pilsbry, 1890a: 405–406, pl. 66, figs. 22–23; “it may be a synonym of *Calliostoma jujubinum*” (Gmelin 1791), from the western Atlantic).
- quadrisulcatus*, *Trochus (Trochus)* – Philippi, 1849h: 124; 1849z3: pl. 38, fig. 8; 1855c: 259–260. Locality unknown. *Calliostoma quadrisulcatus* (Philippi, 1849) (Pilsbry, 1890a: 470, pl. 59, fig. 9; “This species may belong to *C. conuloides*” (Lamarck, 1822), from the eastern Atlantic).
- solidus*, *Trochus* – Philippi, 1849z3: 90–91; 1847z5: pl. 15, fig. 12, *non* Blainville, 1836.

Locality unknown. The uncaptioned plate (1847) appeared two years before the text (1849) making the name available. *Calliostoma laugierii* Payraudeau var. *solidum* (Philippi, 1849), from the eastern Atlantic (Pilsbry, 1890a: 393), but as a junior homonym, it requires renaming if regarded as a valid species or subspecies.

*splendidus*, *Trochus nobilis* var. – Philippi, 1855: 255, 371. Syntype, ZMB 29920 (27.4 mm x 22.5 mm). Synonym of *Calliostoma (Salsipotens) rubiginosum* (Valenciennes, 1846), from Australia (Cotton, 1959: 151–152, fig. 84).

*turricula*, *Trochus* – Philippi, 1851b: 43; 1850q: pl. 44, fig. 19; 1855c: 313–314. Locality unknown; Schultz coll. *Calliostoma turricula* (Philippi, 1851) (Pilsbry, 1890a: 398, pl. 18, fig. 9; “Is it a synonym of *C. exasperatum* Pennant?” from the eastern Atlantic).

*venustus*, *Trochus (Margarita)* – Philippi, 1849h: 126; 1849z3: pl. 37, fig. 16; 1855c: 253. Antilles “?”; Gruner. *Calliostoma venustus* (Philippi, 1849) (Pilsbry, 1890a: 359–360, pl. 67, fig. 72).

*vinctus*, *Trochus* – Philippi, 1843d: 33 [3], pl. 1, fig. 8. Locality unknown. Synonym of *Calliostoma bicingulatum* (Lamarck, 1822), from South Africa (Pilsbry, 1890a: 341).

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“*australis*, *Trochus*” – Cotton (1959: 152) erroneously attributed this species to “Philippi, 1846”, but it was described by Quoy & Gaimard, 1834.

“*conulus*, *Trochus*” – Philippi, 1836a: xii, 175. Correctly on p. xii as “L.” [Linnaeus], indicated on p. 175 as “mihi”, but this was an original combination by Linnaeus (1758) for a species now placed in *Calliostoma*.

“*decoratus*, *Zizyphinus*” – Reeve, 1863c: pl. 4, fig. 28. This species was indicated by Ruhoff (1980: 505) as being by “Philippi, in Reeve,” but it was only based on a ms. name.

“*splendidus*, *Zizyphinus*” – Reeve, 1863c: pl. 2, fig. 11. This species was indicated by Ruhoff (1980: 505) as being by “Philippi, in Reeve,” but it was only based on a ms. name in the Cuming collection.

#### Turbinidae

*armatus*, *Trochus (Calcar)* – Philippi, 1849h: 102; 1850q: pl. 41, fig. 1; 1855c: 277–278. Locality unknown. *Astraliium* (West Indies), possibly a synonym of *A. longispina* (La-



- marck, 1802) (Pilsbry in Tryon & Pilsbry, 1889a: 222, 272, pl. 51, figs. 10–11), or of *Astraea* (*Astralium*) *phoebia* Röding, 1798 (Abbott, 1958: 30–31).
- aster*, *Trochus* – Philippi, 1848k: 57–58; 1847z5: pl. 12, figs. 4, 5. West Indies. The uncaptioned plate (1847) appeared one year before the text (1848) making the name available. Synonym of the western Atlantic *Astralium phoebium* (Röding, 1798) (Abbott, 1958: 30–31).
- bicarinatus*, *Turbo* – Philippi, 1844z4: 74–75, [87], pl. 4, fig. 3, *non* G. B. Sowerby I, 1825, and three other pre-1844 uses. Tertiary of Luithorst, Niedersachsen, Germany [Late Oligocene]. Synonym of *Bolma infausta* (Giebel, 1852) (Anderson, 1959: 67–68, pl. 4, figs. 5a–b; Janssen, 1978a: 28; 1978b: 148, pl. 10, figs. 16–17).
- bronni*, *Delphinula* – Philippi, 1845z: 449 [*nomen nudum*]; 1847-l: 61, pl. 9, fig. 1a–d. Magdeburg area, Germany; Tertiary; Sack's collection. "*Angaria*" *bronni* (Philippi, 1847) (R. Janssen, pers. comm., April 2013).
- buschii*, *Trochus* – Philippi, 1844c: 90 [12], pl. 3, figs. 3, 4; 1849z3: pl. 32, fig. 1; 1851e: 213–214. Panama; Busch coll. Syntypes, SMF 313770 (*n* = 3, Panama) (largest, 20.3 mm x 31.3 mm). The Panamic *Astraea* (*Uvanilla*) *buschii* (Philippi, 1844) (Dall, 1909: 239; Keen, 1971: 354, 356, fig. 155; Abbott & Dance, 1982: 50; Ramírez et al., 2003: 2).
- camprestris*, *Trochus* – Philippi, 1847-l: 62, pl. 9, fig. 9. Magdeburg area, Germany; Tertiary; Sack's collection. Koenen (1892: 861–864) stated that the holotype was from Westeregeln [Saxony-Anhalt, northern Germany] and was in the Dresden Museum. *Turbo camprestris* (Philippi, 1847), Oligocene of Germany (Koenen, 1892: 861–864, pl. 56, fig. 8).
- cingulata*, *Delphinula* "?" – Philippi, 1853d: 24–25, unfigured. Maksur, Red Sea; Hemprich & Ehrenberg. *Cyclostrema cingulata* (Philippi, 1853) (Issel, 1869: 190, 286).
- columellaris*, *Trochus* – Philippi, 1845r: 35 [31], pl. 7, fig. 3; 1848k: pl. 21, fig. 5; 1850q: 123–124. China. Synonym of *Astralium haematragus* (Menke, 1829) (Pilsbry in Tryon & Pilsbry, 1889a: 237).
- concinus*, *Turbo* – Philippi, 1846i: 99; 1847z4: 44–45, pl. 11, fig. 6. Locality unknown; Dunker coll. Synonym of the eastern Asian *Turbo* (*Marmarostoma*) *brunneus* Röding, 1798 (Tomlin, 1936: 138; Higo et al., 1999: 48; Alf & Kreipl, 2003: 15, 27–28), or possibly a synonym of *Turbo* (*Marmarostoma*) *elegans* Menke, 1846 (Alf & Kreipl, 2003: 16).
- cubanus*, *Trochus* (*Calcar*) – Philippi, 1849h: 104; 1850q: pl. 40, fig. 5; 1855c: 274–275. Cuba; Largilliert. Synonym of the western Atlantic *Lithopoma tectum* (Lightfoot, 1786), or as a subspecies thereof (Abbott, 1958: 29).
- ducalis*, *Delphinula* – Philippi, 1845w: 148; 1847z4: 46–47, pl. 11, figs. 9, 10, as *Turbo*. Locality unknown. Synonym of the Indo-Pacific *Turbo lajonkairii* (Deshayes, 1839) (Pilsbry in Tryon & Pilsbry, 1889a: 271).
- dunkeri*, *Delphinula* – Philippi, 1853d: 23, pl. 5, fig. 20. Replacement name for *Delphinula granulosa* Dunker in Krauss, 1848, *non* Grateloup, 1828. Tafel Bay, Cape of Good Hope, South Africa. *Cinysca dunkeri* (Philippi, 1853) (Herbert, 2015: 74).
- elegans*, *Turbo* – Philippi, 1847z4: 64–65, pl. 15, fig. 5. Locality unknown. Synonym of the western Pacific *Turbo* (*Marmarostoma*) *brunneus* Röding, 1798 (Tomlin, 1936: 138; Higo et al., 1999: 48; Alf & Kreipl, 2003: 16, 27–28), or possibly a synonym of *Turbo* (*Marmarostoma*) *elegans* Menke, 1846 (Alf & Kreipl, 2003: 16).
- erythrophthalmus*, *Trochus* (*Calcar*) – Philippi, 1849q: 188–189; 1850q: pl. 45, fig. 3, 3a; 1855c: 315–316. California. Synonym of the Panamic *Astraea* (*Unvanilla*) *olivacea* (W. Wood, 1828) (Keen, 1971: 356–357, fig. 156).
- exiguus*, *Turbo* – Philippi, 1844z4: 56, [87], pl. 4, fig. 2. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. Lectotype, RPMH (Hildesheim), from Freden (designated by Janssen, 1978b: 149, pl. 10, fig. 21). Synonym of *Homalopoma* (*Boutillieria*) *simplex* (Philippi, 1844) (Anderson, 1959: 66–67, pl. 4, figs. 6a–b; Janssen, 1978b: 149, pl. 10, figs. 20–21).
- exilis*, *Turbo* – Philippi, 1847z4: 66, pl. 15, fig. 6, *non* Megerle von Mühlfeld, 1824. Locality unknown. *Leptothyra exilis* (Philippi, 1847) (Pilsbry in Tryon & Pilsbry, 1889a: 257, pl. 62, figs. 3–5), but as a junior homonym, it requires renaming if regarded as a valid species.
- ferrugineus*, *Turbo* – Philippi, 1850p: 75; 1849z2: pl. 17, fig. 7, ex Anton ms. Locality unknown. The specimen and name was supplied by Anton, but Philippi wrote the description. The uncaptioned plate (1849) appeared one year before the text (1850) making the name available. Synonym of *Turbo argyrotomus* Linnaeus, 1758.



- foliaceus*, *Turbo* – Philippi, 1847z4: 41–42, pl. 11, figs. 2, 3, *non* Gmelin, 1791, *non* W. Wood, 1818. New name for *Turbo lamellosus* Philippi, 1846i, *non* Broderip, 1832. *Turbo* (*Marmarostoma*) *laminiferus* Reeve, 1848, from Australia and New Guinea (Alf & Kreipl, 2003: 16, 35).
- globulus*, *Trochus* “?” – Philippi, 1849h: 107; 1849z3: pl. 35, fig. 3; 1851e: 231–232, *non* Röding, 1798. Antillae “?”; Menke. Syntypes, SMF 313723 (n = 2) (Antilles, ex Menke) (larger, 5.3 mm x 5.5 mm). *Leptothyra globulus* (Philippi, 1849) (Pilsbry in Tryon & Pilsbry, 1889a: 262, pl. 62, figs. 10–12, pl. 64, figs. 5–6), but as a junior homonym, it requires renaming if regarded as a valid species.
- gruneri*, *Turbo* – Philippi, 1846i: 98; 1847z4: 52–53, pl. 12, fig. 7. Adelaide, Australia. Type species (OD) of *Euninella* Cotton, 1939, which is regarded by some as a synonym of *Turbo* Linnaeus, 1758. The southern Australian and Tasmanian *Turbo gruneri* Philippi, 1846 (Abbott & Dance, 1982: 47; Wilson, 1993: 105, pl. 12, fig. 15; Wells et al., 2005: 297), or *Turbo* (*Euninella*) *gruneri* Philippi, 1846 (Alf & Kreipl, 2003: 45, pl. 64).
- heliacus*, *Trochus* – Philippi, 1848k: 56–57; 1847z5: pl. 12, figs. 2, 3. The uncaptioned plate (1847) appeared one year before the text (1848) making the name available. West Indies. Synonym of the western Atlantic *Astrarium phoebium* (Röding, 1798) (Abbott, 1958: 30–31).
- hexagonus*, *Trochus* – Philippi, 1850q: 130; 1848k: pl. 22, fig. 6. Locality unknown. The uncaptioned plate (1848) appeared two years before the text (1850) making the name available. *Astrarium hexagonum* (Philippi, 1850) (Pilsbry in Tryon & Pilsbry, 1889a: 237, pl. 64, figs. 44–46, “may be an immature form of *A. haematragum*”); probably distinct from *A. rhodostomum* (Lamarck 1822) (Meyer et al., 2005: 119).
- intercostalis*, *Turbo* – Philippi, 1846i: 98–99, ex Menke ms. Western Australia; Dunker. Synonym of *Turbo pulcher* Reeve, 1842 (Wilson, 1993: 107, pl. 12, fig. 13, as “Menke”).
- laetus*, *Turbo* – Philippi, 1849h: 100; 1849z2: 71–72, pl. 17, fig. 1. “Ostküste Afrikas” (East coast of Africa). *Turbo* (*Euninella*) *laetus* Philippi, 1849, western Indian Ocean (Kilburn, 1972: 398–399; Alf & Kreipl, 2003: 45–46, pl. 65; Herbert, 2015: 70).
- lamarckii*, *Turbo* – Philippi, 1847z4: 55–56, pl. 13, fig. 3. Hawaii, etc. Possible synonym of *Turbo turbinopsis* (Lamarck, 1819) (Pilsbry in Tryon & Pilsbry, 1888a: 199).
- lamellosus*, *Turbo* – Philippi, 1846i: 98, *non* Brocchi, 1814, *non* W. Wood, 1828, *non* Broderip, 1832. Australia; Koch. Renamed *Turbo foliaceus* Philippi, 1847z4, itself also a junior homonym. Synonym of *Turbo squamosus* Gray, 1847 (Wilson, 1993: 107, pl. 12, fig. 8), or of *Turbo* (*Marmarostoma*) *laminiferus* Reeve, 1848, from Australia and New Guinea (Alf & Kreipl, 2003: 16, 35).
- latispina*, *Trochus* – Philippi, 1844c: 90 [12], pl. 3, fig. 2; 1848k: pl. 22, fig. 5; 1850q: 129–130. Locality unknown. *Astraea latispina* (Philippi, 1844) (*Turbinidae*) (Rios, 1994: 42, pl. 13, fig. 142), redescribed by Monteiro & Coelho (2002: 137–143).
- modestus*, *Turbo* – Philippi, 1847z4: 57–58, pl. 13, figs. 7, 8. Locality unknown. *Turbo coronatus* Gmelin, 1791, Indo-Pacific (Pilsbry in Tryon & Pilsbry, 1889a: 217), or *Turbo* (*Lunella*) *coronatus* Gmelin, 1791, from the western Indian Ocean (Alf & Kreipl, 2003: 19, 56–57).
- moluccensis*, *Turbo* – Philippi, 1846i: 99; 1847z4: 44, pl. 11, fig. 5. Amboina; Dunker. Syntype, ZMB 117929 (36.5 mm x 34.3 mm). *Turbo* (*Marmarostoma*) *moluccensis* Philippi, 1846, only known from Indonesia (Alf & Kreipl, 2003: 36, pl. 46, figs. 4–6).
- ochraceus*, *Trochus* – Philippi, 1846i: 101. Locality unknown; Stuttgart coll. Synonym of the eastern Pacific *Astraea* (*Pomaulax*) *gibberosa* (Dillwyn, 1817) (Keen, 1971: 354–355, fig. 152).
- olfersii*, *Trochus* – Philippi, 1850q: 126; 1848k: pl. 22, fig. 1, ex Troschel ms. The uncaptioned plate (1848) appeared two years before the text (1850) making the name available. Philippi prepared the description from a specimen supplied by Troschel. Brazil; Berlin Museum. *Astraea olfersii* (Philippi, 1850) (*Turbinidae*) (Rios, 1994: 42, pl. 13, fig. 143), redescribed by Monteiro & Coelho (2002: 144–146).
- parvulus*, *Turbo* – Philippi, 1849q: 189–190; 1849z2: pl. 19, figs. 15, 16; 1850p: 87–88, *non* Hall, 1845. Liewkiew Island [Ryukyu Islands, Japan]; Cécille via Largilliert. Synonym of the western Pacific *Turbo* (*Marmarostoma*) *stenogyris* P. Fischer, in Kiener, 1873 (Higo et al., 1999: 48; Alf & Kreipl, 2003: 17, 40, pl. 51).
- patulus*, *Turbo* – Philippi, 1849h: 100; 1849z2: 74, pl. 17, fig. 5. China, Philippine Islands. *Turbo setosus* Gmelin var. *patulus* Philippi,



- 1849 (Pilsbry in Tryon & Pilsbry, 1888a: 195, pl. 63, fig. 33).
- paulla*, *Delphinula* – Philippi, 1853d: 24, unfigured. China; Largilliert.
- petrosus*, *Trochus* (*Calcar*?) – Philippi, 1849q: 189. China & Marquesas Islands; Bernardi.
- plicatulus*, *Trochus* (*Calcar*) – Philippi, 1849h: 112; 1849z3: pl. 32, fig. 5; 1851e: 216. Locality unknown; Reents.
- princeps*, *Turbo* – Philippi, 1846t: 134; 1847z4: 61–63, pl. 15, figs. 1, 2, as a synonym of *Turbo argyrostomus* Linnaeus, 1758. No locality given. Synonym of *Turbo* (*Marmarostoma*) *argyrostomus* Linnaeus, 1758 (Higo et al., 1999: 48; Alf & Kreipl, 2003: 15, 24–25).
- psittacinus*, *Turbo* – Philippi, 1845y: 18–19; 1842f: pl. 5, fig. 6. Locality unknown. Philippi's plate, without a caption, was published three years before the text that made this species available. Synonym of the Indian Ocean *Turbo* (*Marmarostoma*) *argyrostomus* Linnaeus, 1758 (Alf & Kreipl, 2003: 15, 24–25).
- pusio*, *Turbo* – Philippi, 1849z2: 71, pl. 16, fig. 10, ex Anton ms. Locality unknown. Credited to Anton by Sherborn (1929: 5315), Philippi made clear that this was just a ms name. *Leptothyra pusio* (Philippi, 1849) (Pilsbry in Tryon & Pilsbry, 1889a: 260, pl. 44, fig. 70).
- reevii*, *Turbo* – Philippi, 1847z4: 48, pl. 12, figs. 1, 2. New name for *Turbo variabilis* Reeve, 1843, *non* Grateloup, 1827. Philippine Islands. Reeve's species name was also preoccupied by Megerle von Mühlfeld, 1824. The western Pacific *Turbo* (*Turbo*) *reevii* (Philippi, 1847) (Abbott & Dance, 1982: 46; Higo et al., 1999: 47; Okutani, 2000: 94–95, fig. 25; Alf & Kreipl, 2003: 15, 22, all as *T. "reeveri"*). However, the spelling of Philippi's substitute name cannot be modified (ICZN Code Article 33.3 (1999)).
- saxosus*, *Trochus* – Philippi, 1850q: 127–128; 1848k: pl. 22, fig. 3. "Perhaps" Mexico. The uncaptioned plate (1848) appeared two years before the text (1850) making the name available. This species is not to be confused with the Panamic *Turbo saxosus* W. Wood, 1828. Synonym of *Astraea tecta* var. *papillata* (Potiez & Michaud, 1838), from the east coast of Mexico (Abbott, 1958: 29).
- scabricula*, *Delphinula* – Philippi, 1844z4: 55, [87], pl. 3, fig. 33. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. Possible senior synonym of *Astraea* (*Lithopoma*) *pustulosa* Münster in Goldfuss, 1844 (Anderson, 1959: 68–70, pl. 2, fig. 9, pl. 4, fig. 4), or a *nomen dubium* (Janssen, 1978b: 148–149).
- tamsiana*, *Delphinula* – Philippi, 1853d: 16–17, pl. 5, fig. 9, ex Dunker ms. Puerto Cabello, [Venezuela]; Tams. This species name was indicated as having been "in literis".
- triumphans*, *Trochus* – Philippi, 1841d: 8; 1843i: 31 [1], pl. 1, fig. 1; 1849z3: pl. 35, fig. 1; 1851e: 229–230. Java; Dunker. The western Pacific *Guldfordia triumphans* (Philippi, 1841) (Ponder, 1971: 133–134, fig. 9; Abbott & Dance, 1982: 49; Higo et al., 1999: 50; Okutani, 2000: 100–101, fig. 50; Qi, 2004: 26, pl. 11E). Type species (SD P. Fischer, 1873) of *Guldfordia* Gray, 1850.
- tuberosus*, *Trochus* – Philippi, 1843h: 69 [9], pl. 2, fig. 11; 1848k: pl. 22, fig. 2; 1850q: 126–127. Locality unknown (1843h); [coast] of Mexico (1850q); Liebman. If from the west coast of Mexico, then it is a possible junior synonym of *Astraea unguis* (W. Wood, 1828), but Abbott (1958: 29) listed it as a synonym of *Astraea tecta* var. *papillata* (Potiez & Michaud, 1838), from the east coast of Mexico.
- venustus*, *Turbo* – Philippi, 1845w: 148; 1847z4: 45–46, pl. 11, figs. 7, 8, *non* Münster in Goldfuss, 1844. Locality unknown. Syntype, ZMB 29902 (27.9 mm x 26.2 mm). Synonym of the Panamic *Turbo* (*Callopoma*) *saxosus* W. Wood, 1828 (Keen, 1971: 351–352, fig. 144; Alf & Kreipl, 2003: 15, 52–53).
- virens*, *Turbo* – Philippi, 1849h: 99; 1849z2: 72–73, pl. 17, fig. 2, ex Anton ms. Locality unknown. Erroneously credited to "Anton, 1849" by Sherborn (1932: 6921) and to "Anton, 1839" by Alf & Kreipl (2003: 16), but Philippi made clear that this was an Anton manuscript name, and we have found no earlier usage by Anton. *Turbo* (*Marmarostoma*) *castaneus* Gmelin, 1791, Caribbean (Pilsbry in Tryon & Pilsbry, 1888a: 203; Alf & Kreipl, 2003: 16).
- winteri*, *Turbo* – Philippi, 1845y: 17–18; 1842f: pl. 5, fig. 2. Java. Philippi's plate, without a caption, was published three years before the text that made this species available. Synonym of the Indian Ocean *Turbo* (*Marmarostoma*) *argyrostomus* Linnaeus, 1758 (Alf & Kreipl, 2003: 15, 24–25).

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"*Astralium*" – Philippi, 1847c: 23. This was listed by Sherborn (1923: 516) as being a separate name from that of Link, 1807, but it was a misuse at most.



"*granosus, Turbo*" – Philippi, 1845y: 17; 1842f: pl. 5, fig. 8. This species was previously described by Martyn, as *Trochus granosus*, in a work that was validated by the ICZN in 1957 (Opinion 479). *Modelia granosa* (Martyn, 1784), from New Zealand.

#### Skeneidae

*elegantula, Delphinula* "?" – Philippi, 1844g: 146, 302, pl. 25, fig. 3. Pezzo, near Rhegium, Calabria, Italy; fossil. *Parviturbo elegantulus* (Philippi, 1844), Pliocene, possibly Recent (Warén, 1992: 154; Rubio et al., 2015: 172, figs. 1A–F); some of the Recent records previously identified as this species are instead *Parviturbo alboranensis* Peñas & Rolán in Peñas et al., 2006.

*exilissima, Delphinula* – Philippi, 1844g: 244, 303, pl. 28, fig. 2; 1853e: 7, pl. 1, fig. 1, as *Skenea exilissima*. Thapsi Peninsula, Sicily, Italy. *Skeneoides exilissima* (Philippi, 1844) (Priolo, 1953a: 101 [99]; Sabelli et al., 1990: 136, both as *Skenea*; Warén, 1992: 156–157). Type species (OD) of *Skeneoides* Warén, 1992.

*laevis, Delphinula* – Philippi, 1844g: 146, 302, pl. 25, fig. 2, 2a, *non* Kiener, 1838. Magnisi Peninsula, Sicily, Italy. Synonym of *Skenea serpuloides* (Montagu, 1808) (Priolo, 1953a: 101 [99], pl. 5, figs. 5–6; Sabelli et al., 1990: 138).

*moelleri, Skenea* – Philippi, 1853f: 9, pl. 1, fig. 5, as *S. mölleri*. Greenland.

*nitens, Delphinula* – Philippi, 1844g: 146, 302, pl. 25, fig. 4, 4a. Carrubbare, Calabria, Italy; fossil. The northeastern Atlantic *Dikoleps nitens* (Philippi, 1844) (Fretter & Graham, 1977: 84–85, figs. 62, 63, as *Skenea*; Sabelli et al., 1990: 136). A transitory secondary junior homonym of *Planaria nitens* I. Lea, 1833 (Thecosomata: Limacinidae), when both species were independently placed in *Cyclostrema* in 1890 and 1923 (Palmer & Brann, 1966: 826); Lea's species is now placed in *Heliconoides* (Janssen, 2012: 154).

#### Colloniidae

*minima, Delphinula* – Philippi, 1844z4: 55, [87], pl. 3, fig. 30. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. *Collonia (Collonia) minima* (Philippi, 1844) (Janssen, 1978a: 29–30; 1978b: 149, pl. 10, fig. 19); now regarded as a *nomen dubium* (R. Janssen, pers. comm., April 2013).

*simplex, Turbo* – Philippi, 1844z4: 56, 74, [87], pl. 4, fig. 4; 1845z: 449. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Lectotype, RPMH (Hildesheim), from Freden (designated by Janssen, 1978b: 149, pl. 10, fig. 20). *Homalopoma (Boutillieria) simplex* (Philippi, 1844) (Anderson, 1959: 66–67, pl. 4, figs. 6a–b; Janssen, 1978b: 149, pl. 10, figs. 20–21).

#### Liotiidae

*exigua, Delphinula* – Philippi, 1849r: 25; 1853c: 21–22, pl. 5, fig. 16. Aden, Red Sea; Th. Philippi. *Cyclostrema exiguum* (Philippi, 1849) (Issel, 1869: 189; Melvill, 1906: 22; Bosch et al., 1995: 39).

*kieneri, Delphinula* – Philippi, 1853d: 22–23, pl. 5, fig. 19, *nom. nov. pro Delphinula cancellata* Kiener, 1838, *non* Gray, 1828. Sibonga, Zebu, Philippines Islands; Cuming coll.

#### Phasianellidae

*adamsi, Phasianella* – Philippi, 1853e: 27, *nom. nov. pro Phasianella brevis* C. B. Adams, 1850, *non* d'Orbigny, 1842, *non* Menke, 1843. *Eulithidium adamsi* (Philippi, 1853), western Atlantic (Redfern, 2013: 27, fig. 72).

*aethiopica, Phasianella* – Philippi, 1853e: 7, pl. 3, figs. 3, 4. Zanzibar, east Africa. *Phasianella aethiopica* Reeve, 1862, ex "Philippi ms", is a distinct species (R. Robertson, note with NHMUK 1963310, Reeve's type specimen), but Reeve's name is a junior homonym and would require renaming if regarded as a valid species. Philippi's species is now regarded as a synonym of *Phasianella solida* (Born, 1778) (Herbert, 2015: 78). Because *P. solida* is the only species of *Phasianella* currently recognized in the western Indian Ocean, it is possible that Reeve's taxon is also a junior synonym of that species (D. G. Herbert, in litt., 28 Jan. 2016).

*amoenula, Phasianella* – Philippi, 1853e: 16, pl. 4, fig. 7. Australia. *Phasianella amoenula* Philippi, 1853 (Pilsbry in Tryon & Pilsbry, 1888a: 180, pl. 39a, fig. 11; Thiele, 1930: 569–570).

*araucana, Phasianella* – Philippi, 1887a: 98 [1887b: 93], pl. 11, fig. 19. Locality unknown, Chile; Francisco J. Ovalle; Tertiary.

*flammulata, Phasianella* – Philippi, 1848c: 18; 1853e: 12–13, pl. 4, fig. 1. Indo-Pacific"?; Ritzmann (1848); Red Sea; Döbler (1853). *Phasianella flammulata* Philippi, 1848 (Pils-



- bry in Tryon & Pilsbry, 1888a: 180, pl. 39a, fig. 9).
- grata*, *Phasianella* – Philippi, 1853e: 9–10, pl. 3, fig. 8. Madagascar; Largilliert. Synonym of *Phasianella variegata* Lamarck, 1822, non Roissy, 1805 (Pilsbry in Tryon & Pilsbry, 1888a: 179, pl. 39a, fig. 14), now *P. solida* (Born, 1778) (Herbert, 2015: 78).
- guttata*, *Phasianella* – Philippi, 1853e: 20–21, pl. 4, fig. 15. Locality unknown. *Phasianella amoenula* Philippi, 1853 (Pilsbry in Tryon & Pilsbry, 1888a: 175, pl. 39a, fig. 16).
- inconspicua*, *Phasianella* – Philippi, 1853e: 21, pl. 4, fig. 16. Locality unknown.
- kochii*, *Phasianella* – Philippi in Krauss, 1848: 104, pl. 6, fig. 4 (January), 1848c: 17–18 (February); 1853e: 26, pl. 5, figs. 9–11. South Africa (Cape region); Koch. Syntype, NHMUK 1923.7.13.19 (13.1 mm x 9.3 mm). *Tricolia kochii* (Philippi in Krauss, 1848), from South Africa (Robertson, 1985: 23–24; Herbert, 2015: 81).
- minima*, *Phasianella* – Philippi, 1860a: 186 [1860b: 168], *nom. nov. pro Phasianella umbilicata* (d'Orbigny, 1841) [*Littorina*], non *Phasianella umbilicata* d'Orbigny, 1842. However, Philippi erroneously renamed the older (1841) name, not the younger (1842) name, undoubtedly unaware of d'Orbigny's actual publication dates, which were not resolved until recently. "*Phasianella (Eulithidium) minima* Philippi, 1860", from the eastern Pacific (Dall, 1909: 238). Some authors incorrectly listed this as a junior synonym of the Peruvian *Tricolia umbilicata* (d'Orbigny, "1840" [*sic*], 1845), but that name is itself preoccupied (Keen, 1971: 358; Marincovich, 1973: 24–25, fig. 46).
- perforata*, *Phasianella* – Philippi, 1849i: 164; 1853e: 20, pl. 4, fig. 14. Panama & Paíta, Peru; E. B. Philippi. The Panamic *Tricolia perforata* (Philippi, 1849) (Keen, 1971: 357–358, fig. 160; Ramírez et al., 2003: 259, both as "1848").
- phasianella*, *Littorina* – Philippi, 1849h: 149–150. Panama; E. B. Philippi. The Panamic *Tricolia phasianella* (Philippi, 1849) (Keen, 1971: 357–358, fig. 161; Ramírez et al., 2003: 259).
- pygmaea*, *Phasianella* – Philippi, 1848c: 18–19; 1853e: 18, pl. 4, fig. 11. Locality unknown. *Nomen dubium* (Robertson, 1985: 25, "This is probably a *Tricolia*, but I consider it a *nomen dubium*").
- splendida*, *Phasianella* – Philippi, 1849s: 30–31; 1853e: 8–9, pl. 3, fig. 6. Red Sea; Bernardi. Synonym of *Phasianella variegata* Lamarck, 1822 (Pilsbry in Tryon & Pilsbry, 1888a: 179, pl. 39a, fig. 15).
- strigata*, *Phasianella* – Philippi, 1853e: 15–16, pl. 4, fig. 6. Locality unknown. Synonym of the eastern Atlantic *Phasianella pulla* (Linnaeus, 1758) (Pilsbry in Tryon & Pilsbry, 1888a: 168, pl. 39a, fig. 13).
- tenuis*, *Phasianella* – Philippi, 1844n: 110. Palermo & Syracuse, Sicily, Italy. Synonym of *Phasianella pulla* (Linnaeus, 1758) (Pilsbry in Tryon & Pilsbry, 1888a: 168).
- turgida*, *Phasianella* – Philippi, 1853e: 5–6, pl. 2, figs. 7–10, pl. 5, fig. 4. West coast of Australia. Synonym of *Phasianella ventricosa* Quoy & Gaimard, 1833 (Pilsbry in Tryon & Pilsbry, 1888a: 165; Pritchard & Gatliff, 1902: 112–113).

### Helicinidae

- bronniana*, *Helicina* – Philippi, 1847r: 124. Hawaii; Bronn. *Helicina (Pleuropoma) bronniana* Philippi, 1847 (Cowie et al., 1995: 20).
- columbiana*, *Helicina* – Philippi, 1847r: 126–127. Colombia; Brandt. Syntype, ZMB 104640 (8.0 mm x 9.5 mm) (Richling & Glaubrecht, 2008: 284, fig. 4a). *Helicina (Tamsiana?) columbiana* Philippi, 1847.
- crassilabris*, *Helicina* – Philippi, 1847r: 125–126. Hawaii. Sykes (1900: 397) concluded that this species "really comes from Venezuela or the Caribbean Region" (see also Neal, 1934: 99; Cowie et al., 1995: 23).
- hornbeckii*, *Helicina* – Philippi, 1847r: 125. St. Thomas, Virgin Islands; Hornbeck. Two syntypes, ZMB 103729 (ex Hornbeck); two possible syntypes, ZMB 103728 (ex Dunker) (Richling & Glaubrecht, 2008: 291, fig. 3e). Junior synonym of *Helicina striata* Lamarck, 1822.
- menkeana*, *Helicina* – Philippi, 1847r: 126. Locality unknown. Type material not found in ZMB (Richling & Glaubrecht, 2008: 272).
- nicobarica*, *Helicina* – Philippi, in Pfeiffer, 1847: 149–150. Nicobar Island; Th. Philippi.
- pisum*, *Helicina* – Philippi, 1847r: 124–125, non Hombron & Jacquinot, 1846 (Tahiti). Hawaii; Largilliert. Sykes (1900: 397) concluded that the type locality ("Insulae Sandwich") was an error, and the species was probably from the Savage Islands (Ilhas Selvagens, North Atlantic), "from which specimens, inseparable from this, undoubtedly do come" (see also Neal, 1934: 99; Cowie et al., 1995: 23).



## Neritidae

*aspera*, *Neritina* – Philippi, 1845i: 63. “China?”

Synonym of *Neritina* (*Clithon*) *brevispina* Lamarck, 1822, from the south Pacific (Tryon in Tryon & Pilsbry, 1888a: 65, pl. 24, fig. 23).

*bicanalis*, *Neritina* – Philippi, 1845i: 64; 1849i: 160. Tahiti; Largilliert. Seemingly described a second time in 1849, which did not mention the 1845 account. Synonym of *Neritina* (*Clypeolum*) *canalis* G. B. Sowerby I, 1825 (Tryon in Tryon & Pilsbry, 1888a: 57, pl. 18, fig. 8).

*brandtii*, *Neritina* – Philippi, 1849i: 161. Locality unknown; Brandt. Synonym of *Neritina* (*Clypeolum*) *beckii* (Récluz, 1841), from the Philippines and Indonesia (Tryon in Tryon & Pilsbry, 1888a: 58).

*carbonaria*, *Nerita* – Philippi, 1844b: 84–85 [2–3]. Locality unknown. Synonym of *Nerita morio* (G. B. Sowerby I, 1833), Indo-Pacific (Tryon in Tryon & Pilsbry, 1888a: 33, pl. 8, fig. 41).

*chilensis*, *Nerita* – Philippi, 1887a: 98 [1887b: 92–93], pl. 11, fig. 18. Matanzas, Chile; Tertiary [Miocene]. Holotype, SGO.PI.844. *Nerita* (*Heminerita*) *chilensis* Philippi, 1887 (Nielsen et al., 2004: 86–87, figs. 73–75).

*chloroleuca*, *Nerita* – Philippi, 1848b: 14–15. Locality unknown. Possibly a synonym of the Indo-Pacific *Nerita chamaeleon* Linnaeus, 1758 (Tryon in Tryon & Pilsbry, 1888a: 20).

*circinata*, *Neritina* – Philippi, 1849i: 161. Pacific Ocean; E. B. Philippi. Synonym of *Neritina* (*Clypeolum*) *bruguieri* Récluz, 1841 (Tryon in Tryon & Pilsbry, 1888a: 58).

*cirrata*, *Neritina* – Philippi, 1845i: 64. “China?” Synonym of *Neritina* (*Clypeolum*) *bruguieri* Récluz, 1841 (Tryon in Tryon & Pilsbry, 1888a: 58).

*elongata*, *Nerita* – Philippi, 1844g: 139, 302, pl. 24, fig. 20. Taranto, Italy; fossil [Plio-Pleistocene].

*largillierti*, *Nerita* – Philippi, 1849i: 160. Gabon in Guinea; Largilliert. Syntype, MNHN Paris (n = 1) (14.3 mm x 14.4 mm); a second lot in MNHN Paris (ex Largilliert), but with a note that this lot is a “dubious record, perhaps *N. senegalensis* [and] 1 *N. chamaeleon*” (C. Krijnen, 1999 note). Synonym of *Nerita senegalensis* Gmelin, 1791 (Tryon in Tryon & Pilsbry, 1888a: 22).

*lugubris*, *Neritina* – Philippi, 1843b: 29–30 [5–6], pl. 1, fig. 9, *non* Lamarck, 1822. Oahu, Hawaii. Homonym replaced as *Nerita affinis* Récluz, 1850, but both are now regarded as

synonyms of *Neripteron cariosus* (W. Wood, 1828) (Kay, 1979: 66, fig. 20C, D; Severns, 2011: 60–61).

*meridionalis*, *Nerita* – Philippi, 1836a: xi, 159–160, pl. 9, fig. 13; 1844g: 138, 302, pl. 24, fig. 19. Sicily, in rivers. Syntypes, SMF 261198 (n = 7); SMF 26199 (n = 3); SMF 304613 (n = 4) (all from Sicily). *Theodoxus* (*Theodoxus*) *meridionalis* (Philippi, 1836) (Zettler & Richard, 2003).

*peruviana*, *Nerita* – Philippi, 1844b: 84 [2], pl. 1, fig. 4. “Peru”; E. B. Philippi. Syntypes, MNHNS 1131 (n = 1, 16.2 mm x 16.7 mm); SMF 304756 (labeled as from “China”) (largest, 16.3 mm x 16.3 mm). Synonym of *Nerita yoldii* Récluz, 1841, from the Indo-Pacific (Dall, 1909: 288).

*ringicula*, *Nerita* – Philippi, 1851c: 86–87. Locality unknown. Syntypes SMF 304747 (n = 2, no locality) (10.4 mm x 9.3 mm; 9.1 mm x 8.7 mm). An indeterminate species (Tryon in Tryon & Pilsbry, 1888a: 35).

*scabrella*, *Nerita* – Philippi, 1848b: 14–15. Locality unknown. An indeterminate species (Tryon in Tryon & Pilsbry, 1888a: 35).

*winteri*, *Nerita* – Philippi, 1844b: 86 [4], pl. 1, fig. 10. Moluccas. *Nerita winteri* Philippi, 1844 (Tryon in Tryon & Pilsbry, 1888a: 25, pl. 9, fig. 73).

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“*birmanica*, *Nerita*” – Troschel, 1878: 190, pl. 17, fig. 6, ex Philippi ms. Syntypes, SMF 304722 (n = 2) (Burma). Some authors attributed this species solely to Philippi (e.g., Tryon, 1888: 32, pl. 8, fig. 29; Berry et al., 1973: 189).

“*incerta*, *Nerita*” – Philippi, 1844b: 85 [3], pl. 1, fig. 6. This species was credited to Busch, and the description was signed by him. Thus, its attribution to Philippi by Okutani (2000: 104–105, fig. 21), is not correct.

## Ampullariidae

*Pachychilus* – Philippi, 1851d: 7, *non* I. Lea & H. C. Lea, 1851, unnecessary replacement name for *Pachylabra* Swainson, 1840, which Philippi rejected on grammatical grounds (ICZN Code Article 32, especially 32.2 (1999)). Both Philippi’s name and Swainson’s name are junior synonyms of *Pila* Röding, 1798 (e.g., Wenz, 1939: 503; Cowie, 2015: 28), while the unrelated *Pachychilus* Lea & Lea, 1851, is a valid taxon in the Pachychilidae (freshwater Cerithioidea) (Wenz, 1939: 685).



*aperta*, *Ampullaria* – Philippi, 1849r: 18; 1851d: 14, pl. 3, fig. 5. Locality unknown. Possible syntypes, MNHNS 15935, 15896 (identified by S. Thiengo in 2008; Cowie, 2015: 53). *Pila aperta* (Philippi, 1849) from Burma (Prashad, 1925: 88–89, pl. 15, figs. 1–2; Cowie & Thiengo, 2003: 80). The MNHNS material, labeled as coming from Venezuela, may represent a South American species of *Pomacea*, in which case the "Burma" records would be in error (Cowie, 2015: 53).

*balteata*, *Ampullaria* – Philippi, 1851d: 21–22; pl. 5, fig. 7; 1852a: 22–23; 1852b: pl. 17, fig. 4. Locality unknown [Trinidad – Baker, 1930: 25]. Type restricted to first figure (Baker, 1930: 25). Synonym of *Pomacea (Effusa) glauca* (Linnaeus, 1758) (Cowie & Thiengo, 2003: 52).

*borneensis*, *Ampullaria* – Philippi, 1852a: 24; 1852b: 31, pl. 8, fig. 3. Borneo; Largilliert. Possible syntype, MNHNS 15948 (identified by S. Thiengo in 2008; Cowie, 2015: 29). Synonym of *Pila scutata* (Mousson, 1848) (Brandt, 1974: 52).

*cecillii*, *Ampullaria* – Philippi, 1849q: 191; 1852b: 47, pl. 13, fig. 6, as *A. "cecillei."* Nossibe [Noss-ibé, Madagascar]; Largilliert. NHMUK 1893.6.30.130–132 (ex Morelet); MCZ 146107 (n = 2); NMWZ 1981.118.00133 (n = 2); NMWZ 1981.118.03468 (n = 2), labeled as "syntypes" or "paratypes" of *A. cecillii*, but may instead represent the type material of *Ampullaria inops* Morelet, 1851 (figured by Brown, 1994: 56, fig. 24) (Cowie, 2015: 31). Possible syntypes, Muséum de Rouen 20140280 (n = 5, from Nossy-be, but without original label); MNHNS 15899 (formerly 61.057) (identified by S. Thiengo in 2008; smaller specimen may be *A. exigua* Philippi; Cowie, 2015: 31); MNHNS 15955 (formerly 61.090). *Pila (Pila) cecillei* (Philippi, 1849) from Madagascar (Starmühlner, 1969: 119–158; Brown, 1994: 56–57, figs. 24e–f; Fischer-Piette & Vukadinovic, 1973: 349–351, all as "1848"). Although the original spelling was "cecillii", nearly all subsequent usages, including Philippi (1852b: 47) used "cecillei" which is the prevailing usage, and is therefore preserved as the correct original spelling (ICZN Code Article 33.3.1 (1999); Cowie, 2015: 31).

*chemnitzii*, *Ampullaria* – Philippi, 1852a: 25; 1852b: 39–40, pl. 10, fig. 5. Based, among other things, on Chemnitz (1786: pl. 128, fig. 1135). Locality unknown [restricted to Tucacas, Venezuela – Baker, 1930: 5].

Type restricted to Philippi's figure (Baker, 1930: 5). *Pomacea (Pomacea) chemnitzii* (Philippi, 1852), from Ecuador, Colombia, and Venezuela (Baker, 1930: 5–6; Cowie & Thiengo, 2003: 59).

*cingulata*, *Ampullaria* – Philippi, 1851d: 19, pl. 5, fig. 3; 1852a: 22. Locality unknown. Lectotype, ZMB 1376 (no locality) (33.9 mm x 30.3 mm), designated by Köhler & Glaubrecht (2006: 201, fig. 1F). *Pomacea (Effusa) cingulata* (Philippi, 1851) but of uncertain status (Cowie & Thiengo, 2003: 50).

*columbiensis*, *Ampullaria* – Philippi, 1851d: 20–21, pl. 5, fig. 5, ex Sowerby ms. Locality unknown; western Colombia on label. Lectotype, ZMB 1343a ("Westkolumbien, coll. Cuming") (35.3 mm x 30.4 mm), designated by Köhler & Glaubrecht (2006: 202, fig. 1G), and 1 paralectotype, ZMB 1343b. *Pomacea columbiensis* (Philippi, 1851) (Cowie & Thiengo, 2003: 60).

*crocostoma*, *Ampullaria* – Philippi, 1852a: 26; 1852b: 42–43, pl. 12, fig. 3. Caracas, Venezuela; Tams. Type material not found in ZMB (Köhler & Glaubrecht, 2006: 203), or elsewhere (Cowie & Thiengo, 2003); although Cowie & Thiengo (2003: 52) listed ZMB 109501 (n = 3) as "possible syntypes" (those specimens originate from the same collector, "Porto Cabello, Venezuela, leg. Tams, coll. Dunker" and may be appropriate for the designation of a neotype if deemed necessary, R. Cowie, in litt., 9 Dec. 2014). Cowie (2015: 63) suggested that MNHNS 15917 (formerly 61.044) (n = 1, 35.2 mm x 38.2 mm), although labeled as "*Ampullaria pachystoma*", does not match the figure or original dimensions, and may instead be the figured type of *A. crocostoma* Philippi. Synonym of *Pomacea (Effusa) glauca* (Linnaeus, 1758) (Cowie & Thiengo, 2003: 52–53).

*dolium*, *Ampullaria* – Philippi, 1852a: 25–26; 1852b: 40, pl. 11, fig. 1. Orinoco, Guyana. Synonym of *Pomacea (Pomacea) urceus* (Müller, 1774) (Baker, 1930: 2; Cowie & Thiengo, 2003: 62).

*dorbignyana*, *Ampullaria* – Philippi, 1852b: 49, as *A. "d'orbigny"*, 65–66, pl. 21, fig. 4. Based on a figure in d'Orbigny (1835: pl. 4, fig. 4). La Plata, Argentina. Synonym of *Pomacea (Pomacea) canaliculata* (Lamarck, 1822) (Cowie & Thiengo, 2003: 62), who selected the better known original spelling.

*exigua*, *Ampullaria* – Philippi, 1852a: 26–27; 1852b: 46, pl. 13, fig. 4. Locality unknown.



- Possible syntype, MNHNS 15889 ( $n = 2$ ) (identified by S. Thiengo in 2008; Cowie, 2015: 36). *Pila exigua* (Philippi, 1852) from Egypt, or a junior synonym of *Pila ovata* (Olivier, 1804); earlier records from South America are in error (Pain, 1952: 287; Cowie & Thiengo, 2003: 80; Cowie, 2015: 36).
- fuliginea*, *Ampullaria* – Philippi, 1852a: 27–28; 1852b: 53–54, pl. 16, fig. 6, ex Koch ms. Locality probably Madagascar; Koch. Synonym of *Pila cecillei* (Philippi, 1849) (Starmühlner, 1969: 119; Cowie, 2015: 37).
- geveana*, *Ampullaria* – Philippi, 1852a: 26; 1852b: 26, pl. 7, fig. 2. Unjustified emendation of *Ampullaria gevesensis* Deshayes, 1838, from northern South America (ICZN Code Article 32.5.1 (1999); Cowie & Thiengo, 2003: 53), itself now a synonym of *Pomacea (Effusa) glauca* (Linnaeus, 1758).
- gruneri*, *Ampullaria* – Philippi, 1852a: 24–25; 1852b: 37, pl. 9, fig. 8. Locality unknown; Gruner. Synonym of *Pila ampullacea* (Linnaeus, 1758), southeast Asia (Brandt, 1974: 49; Cowie, 2015: 38).
- impervia*, *Ampullaria* – Philippi, 1851d: 17, pl. 4, fig. 7; 1852a: 21. Brazil. Syntype, ZSM 20012067 (Cowie & Thiengo, 2003: 47). Synonym of *Asolene crassa* (Swainson, 1823) (Cowie & Thiengo, 2003: 47).
- knorrii*, *Ampullaria* – Philippi, 1852a: 28; 1852b: 57, pl. 18, fig. 3. Trinidad; Gruner. MNHNS 15877 (formerly 61.043) is labeled as coming from Anton, not Gruner, so probably not type (R. Cowie, in litt., 14 Oct. 2014; Cowie, 2015: 62). Synonym of *Marisa cornuarietis* (Linnaeus, 1758) (Baker, 1930: 26) or of *Marisa fasciatus* (Guilding, 1828) (Cowie & Thiengo, 2003: 51).
- kordofana*, *Ampullaria* – Philippi, 1852b: 44–45, pl. 13, fig. 1, ex Parreyss ms. Kordofan [Sudan]. Possible syntypes, MNHNS 15902 ( $n = 1$ ) (identified by S. Thiengo in 2008); SMF 344089 ( $n = 2$ ) (Cowie, 2015: 39). This species was indicated as being “in lit.”, so Philippi is considered to be its author. Synonym of *Pila ovata* (Olivier, 1804) (Pain, 1952: 286; Cowie, 2015: 39).
- labiosa*, *Ampullaria* – Philippi, 1852b: 58, pl. 18, fig. 5, ex Koch ms. Locality unknown. Synonym of *Pomacea (Pomacea) flagellata* (Say, 1829), from Central America (Cowie & Thiengo, 2003: 67), or as *incertae sedis* (Cowie, 2015: 54).
- lamarckii*, *Ampullaria* – Philippi, 1852b: 67, pl. 21, fig. 5. Locality unknown. Probable figured syntype, MNHNS 15886 (formerly 61.040) (identified by S. Thiengo in 2008; Cowie, 2015: 62). Synonym of *Pomacea (Pomacea) flagellata* (Say, 1829), from Central America (Cowie & Thiengo, 2003: 67).
- largillierti*, *Ampullaria* – Philippi, 1849q: 192; 1852b: 46–47, pl. 13, fig. 5. Nossibe [Nossibé, Madagascar]; Largilliert. Syntypes, MNHNS 15889 ( $n = 1$ , 32.2 mm x 31.1 mm); MCZ 146108 ( $n = 2$ ). Synonym of *Pila (Pila) cecillei* (Philippi, 1849) from Madagascar (Starmühlner, 1969: 119–158; Fischer-Piette & Vukadinovic, 1973: 349–351, both as “1848”; Cowie, 2015: 39).
- linnaei*, *Ampullaria* – Philippi, 1852a: 29; 1852b: 62, pl. 20, fig. 6. Locality not stated. Philippi stated that Sylvanus Hanley sent him a drawing of a specimen of “*Helix ampullacea* Linnaeus” from the Linnean collection in London. Philippi subsequently obtained a specimen from an unknown source that he initially thought was the Linnean species, but he later determined that this specimen was instead a new species. Possible type material, MNHNS 15945 (identified by S. Thiengo in 2008; Cowie, 2015: 54). Synonym of *Pomacea (Pomacea) lineata* (Spix, 1827), from northeastern South America (Cowie & Thiengo, 2003: 67), or of *Pila ampullacea* (Linnaeus, 1758), from Thailand (Brandt, 1974: 49); further research is required.
- lucida*, *Ampullaria* – Philippi, 1852b: 45, pl. 13, fig. 2, pl. 14, fig. 4, ex Parreyss ms. Egypt. This species was indicated as being “in lit.”, so Philippi is considered to be its author. Possible syntype, MNHNS 15870 (identified by S. Thiengo in 2008; Cowie, 2015: 40). Synonym of *Pila ovata* (Olivier, 1804) (Pain, 1952: 287).
- magnifica*, *Ampullaria* – Philippi, 1852a: 29, ex Dunker ms.; 1852b: 64–65, pl. 21, fig. 1 Java. *Pila ampullacea* (Linnaeus, 1758) (Brandt, 1974: 49; Cowie, 2015: 41).
- malabarica*, *Ampullaria* – Philippi, 1852a: 24; 1852b: 29, pl. 7, fig. 8. Mangalore, Malabar. Syntype, MNHNS 15926 (formerly 61128) ( $n = 1$ , 36.1 mm x 31.9 mm) (probable figured specimen, Cowie, 2015: 41). Synonym of *Ampullaria virens* Lamarck, 1822 (Cowie, 2015: 41).
- melanostoma*, *Ampullaria reflexa* – Philippi, 1852b: 35, 58, pl. 18, fig. 4, ex Parreyss ms. Mexico. Possible syntype, ZMB 109500 (Mexico, coll. Dunker) (41.2 mm x 37.4 mm) (Köhler & Glaubrecht, 2006: 207). Synonym of *Pomacea (P.) flagellata* (Say, 1829) (Cowie & Thiengo, 2003: 69).



- nigrilabris*, *Ampullaria* – Philippi, 1852a: 29; 1852b: 65, pl. 21, fig. 2. Locality unknown. Brazil, possibly a good species: *Pomacea* (*Pomacea*) *nigrilabris* (Philippi, 1852) (Cowie & Thiengo, 2003: 70; Simone, 2006: 56, fig. 96, as “1851”).
- nucleus*, *Ampullaria* – Philippi, 1852a: 23; 1852b: 25–26, pl. 7, fig. 1. Locality unknown; Berlin Museum. Lectotype, ZMB 1374a (17.4 mm x 15.6 mm), designated by Köhler & Glaubrecht (2006: 207–208, fig. 2H); one paralectotype, ZMB 1374b (15.9 mm x 13.9 mm). Ampullariidae of uncertain status, “included here as a New World species” (Cowie & Thiengo, 2003: 79; Cowie, 2015: 63).
- orientalis*, *Ampullaria* – Philippi, 1849q: 192. Java, Philippines; China – Largilliert. Possible syntypes, MNHNS 15915 (formerly 61.050) (n = 1, from Java, 40.2 mm x 38.8 mm); MNHNS 15944 (formerly 61.055) (n = 1, from China, 29.3 mm x 27.1 mm); MNHNS 15932 (formerly 61.072) (n = 2, from China, larger is 38.9 mm x 33.6 mm); MNHNS 15937 (formerly 61.092) (n = 1, from Philippines, 37.5 mm x 31.4 mm); SMF 344087 (n = 1); MNHNS 15914 (formerly 61.094); MNHNS 15916 (formerly 61.086); MNHNS 15960 (formerly 61.077) (identified by S. Thiengo in 2008; Cowie, 2015: 45, “the material in the Philippi collection ... labeled as *orientalis* Philippi appears to belong to more than one species and may not all be type material”). Synonym of *Pila scutata* (Mousson, 1848) (Brandt, 1974: 52).
- pachystoma*, *Ampullaria* – Philippi, 1849r: 17; 1852b: 44, pl. 12, fig. 5. Brazil. MNHNS 15917 (formerly 61.044) (n = 1, 35.2 mm x 38.2 mm), although labeled as this species, does not match the figure or original dimensions, and may instead be the figured type of *A. crocostoma* Philippi (R. Cowie, in litt., 14 Oct. 2014; Cowie, 2015: 63). Synonym of *Pomacea* (*Effusa*) *glauca* (Linnaeus, 1758) (Cowie & Thiengo, 2003: 55); type locality probably in error.
- pallens*, *Ampullaria* – Philippi, 1849r: 17–18; 1852b: 32, pl. 8, fig. 4. East Indies. Figured syntype, MNHNS 15921 (formerly 61.051) (n = 1, 40.7 mm x 37.7 mm). Probably a synonym of *Pila virens* (Lamarck, 1822); earlier records from Mexico are in error (Cowie & Thiengo, 2003: 80; Cowie, 2015: 45).
- phaeostoma*, *Ampullaria* – Philippi, 1852a: 26; 1852b: 45–46, pl. 13, fig. 3. Locality unknown. Possible syntype, MNHNS 15919 (formerly 61.035) (Cowie, 2015: 63). *Pomacea* (*Pomacea*) *flagellata* (Say, 1829), from Central America (Cowie & Thiengo, 2003: 72).
- planorbula*, *Ampullaria* – Philippi, 1852a: 23; 1852b: 26–27, pl. 7, fig. 3. Locality unknown; Berlin Museum. Lectotype, ZMB 2131 (15.8 mm x 20.7 mm), designated by Köhler & Glaubrecht (2006: 208, fig. 3B). Group of *Pomacea* (*Effusa*) *glauca* (Linnaeus, 1758) (Cowie & Thiengo, 2003: 55); *Pomacea planorbula* (Philippi, 1852) (Ramírez et al., 2003: 271; Simone, 2006: 58, fig. 105, both as “1851”).
- pomum*, *Ampullaria* – Philippi, 1851d: 13–14, pl. 3, figs. 3, 4; 1852a: 20–21. Locality unknown. Possible syntype, MNHNS 15890 (formerly 195) (R. Cowie, 2015: 63). Unknown species (Cowie & Thiengo, 2003: 72–73).
- pyrum*, *Ampullaria* – Philippi, 1851d: 18–19, pl. 5, fig. 2; 1852a: 21–22. Brazil; Munich Museum. ZSM 20012060, syntype. *Pomacea* (*Pomacea*) of uncertain status; type locality may be in error (Cowie & Thiengo, 2003: 73).
- retusa*, *Ampullaria* – Philippi, 1851d: 18, pl. 5, fig. 1, ex Olfers ms; 1852a: 21. Río Rapunin, Guyana, & Brazil. There is no evidence that Olfers provided anything but the specimens and the name, so Philippi must be regarded as the author. Lectotype, ZMB 1339 (59.6 mm x 53.9 mm), designated by Köhler & Glaubrecht (2006: 210, fig. 3F); “doubtful” paralectotypes, MNHNS 15936 (formerly 61.073) (n = 2) (Cowie, 2015: 64). *Pomacea* (*Pomacea*) *retusa* (Philippi, 1851), of uncertain status (Cowie & Thiengo, 2003: 74). Although some previous authors synonymized Philippi’s species with *Pomacea flagellata* (Say, 1829), Pain (1964) and others determined that Say’s species is from Central America, and is not found in Guyana or Brazil, type locality of Philippi’s species.
- robusta*, *Ampullaria* – Philippi, 1852b: 50–51, pl. 15, figs. 4, 5. Locality unknown. Figured (?) syntype, MNHNS 15879 (formerly 61.063) (n = 1, 58.1 mm x 49.9 mm). Synonym of *Pomacea* (*Pomacea*) *columellaris* (Gould, 1848), from Peru and Bolivia (Cowie & Thiengo, 2003: 74).
- rugosa*, *Ampullaria* – Philippi, 1851d: 20, ex Parreyss ms, *non* Lamarck, 1801. Unavailable name; published in synonymy of *Ampullaria wernei* Philippi, 1851, and not treated as an available name or adopted as the name of a taxon before 1961 (ICZN Code Article 11.6 (1999)) (Cowie, 2015: 47).
- speciosa*, *Ampullaria* – Philippi, 1849r: 18; 1852b: 40–41, pl. 11, fig. 2. East Indies. Possible syntype, MNHNS 15900 (formerly 61.042) (n = 1, 53.9 mm x 30.8 mm); ZMB



- 1323 (66.4 mm x 59.0 mm) (Köhler & Glaubrecht, 2006: 210–211). Both lots from “Kap [or Cap] Gardafui” = Cape Guardafui, Ras Asir, Somalia. *Pila speciosa* (Philippi, 1849), restricted to “Somaliland” (east Africa) (Pain, 1949; Cowie 2015: 48).
- sumatrensis*, *Ampullaria* – Philippi, 1852a: 28; 1852b: 59, pl. 19, figs. 1–2. Danu-luar River, Sumatra. Synonym of *Pila ampullacea* (Linnaeus, 1758) (Brandt, 1974: 49; Cowie, 2015: 50).
- swainsoni*, *Ampullaria* – Philippi, 1852b: 53, pl. 16, fig. 5. Based on Swainson (1831: pl. 64, *Ampullaria fasciata* var.). Locality unknown [Brazil]. *Pomacea* (*Pomacea*) *swainsoni* (Philippi, 1852) (Cowie & Thiengo, 2003: 75; Simone, 2006: 62, fig. 120). Swainson’s figured specimen may be in the Manchester Museum (Cowie & Thiengo, 2003: 75). Alderson (1926) aptly noted that “the history of *A. swainsoni* is an unbroken chain of errors,” yet he created a new error in concluding that Hanley (1854) had described a junior homonym with that name; actually, Hanley had specifically attributed this species to Philippi (Cowie & Thiengo, 2003: 66; Coan & Kabat, 2012: 325).
- tamsiana*, *Ampullaria* – Philippi, 1852a: 27; 1852b: 51, pl. 16, figs. 1, 2, ex Dunker ms. Puerto Cabello; Tams. The name was indicated as being “in lit.”. Lectotype, ZMB 109502 (Porto Cabello, Venezuela) (37.8 mm x 39.4 mm), designated by Köhler & Glaubrecht (2006: 211–212, fig. 3J); paralectotypes, ZMB 111746 (n = 3) (same locality); “potential” paralectotypes, ZMB 109.503 (n = 2) (Venezuela). Synonym of *Pomacea* (*Effusa*) *glaucia* (Linnaeus, 1758) (Cowie & Thiengo, 2003: 56).
- teres*, *Ampullaria* – Philippi, 1849r: 19; 1852b: 38–39, pl. 10, fig. 4. Locality unknown. Syntype, ZMB 109504; possible syntype, MNHNS 15958 (formerly 178) (identified by S. Thiengo in 2008; Cowie, 2015: 65). Synonym of *Pomacea* (*Effusa*) *glaucia* (Linnaeus, 1758), from tropical America (Cowie & Thiengo, 2003: 56).
- unicolor*, *Ampullaria gigas* – Philippi, 1852b: 47, pl. 10, fig. 2. Locality unknown. *Pomacea* (*Pomacea*), but species assignment uncertain (Cowie & Thiengo, 2003: 76).
- wernei*, *Ampullaria* – Philippi, 1851d: 19–20, pl. 5, fig. 4; 1852a: 22; 1852b: 54, pl. 17, fig. 2. White Nile. Lectotype, ZMB 1335 (69.9 mm x 62.3 mm) (designated by Köhler & Glaubrecht, 2006: 212, fig. 3L); paralectotype, specimen figured in 1852b: pl. 17, fig.

2, which is probably MNHNS 15962 (Cowie, 2015: 52). *Pila wernei* (Philippi, 1851), from Africa (Brown, 1994: 56).

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“*castanea*, *Ampullaria*” – Baker (1930: 14) noted the use of this name by Philippi (1852b: 41, pl. 12, fig. 1) “*non* Deshayes 1830” (i.e., a misidentification by Philippi) and renamed Philippi’s misidentified specimens as *Ampullaria philippiana*. Cowie & Thiengo (2003: 52, 55) determined that *philippiana* Baker and *castanea* Deshayes were both junior synonyms of *Pomacea* (*Effusa*) *glaucia* (Linnaeus, 1758).

#### Cyclophoridae *sensu lato*

- euomphalum*, *Cyclostoma* – Philippi, 1851b: 30–31. Locality unknown.
- menkeanum*, *Cyclostoma* – Philippi, 1847r: 123–124. Locality unknown. *Cyclophorus* (*Litostylus*) *menkeanum* (Philippi, 1847), from Sri Lanka (Kobelt, 1902: 100); as *Litostylus* is a junior homonym, it was replaced by *Kobeltostylus* Egorov, 2006 (Egorov & Greke, 2007: 61).
- speciosum*, *Cyclostoma* – Philippi, 1847r: 123. Locality unknown. *Salpingophorus speciosum* (Philippi, 1847), from Burma and Thailand (Kobelt, 1902: 133); the species placed by Kobelt in *Salpingophorus* are now referred to either *Cyclophorus* (C.) or *Cyclophorus* (*Glossostylus*) (Egorov & Greke, 2007: 57–58).
- variegatum*, *Cyclostoma* – Philippi, 1844h: 104 [2], pl. 1, fig. 3, ex Valenciennes ms. Java. *Salpingophorus perdix* (Broderip & G. B. Sowerby I, 1830), from Java and Sumatra (Kobelt, 1902: 131), or as *Cyclophorus* (C.) *perdix* (Broderip & G. B. Sowerby, I, 1830) (Egorov & Greke, 2007: 57–58).

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“*pulverulentum*, *Cyclostoma*” – Pfeiffer, 1854: 301–302, pl. 40, figs. 13, 14, ex Philippi ms. This species was listed by Girardi (1978: 216) and Ruhoff (1980: 451) as being by “Philippi, in Pfeiffer,” but it is indicated by Pfeiffer as being only a ms name; now a synonym of *Ostodes plicata* (Gould, 1848) (Poteriidae).

#### Viviparidae

- araucana*, *Paludina* – Philippi, 1887a: 79 [1887b: 74], pl. 9, fig. 10. Puchoco, Chile;



Tertiary. Syntypes, SGO.PI.4648–4653 (n = 1 specimen each). Prashad (1928: 223) stated that this “species has not been found since, and has been generally considered to be a doubtful member of the family [Viviparidae] as now restricted,” but the subsequent description by Doello-Juando of a Cretaceous species of *Viviparus* from Argentina, which “appears to belong to the same group as Philippi’s species ... prove[s] that the family was represented in South America from at least the Upper Cretaceous to the early Tertiaries.” Parodiz (1969: 128, pl. 14, fig. 1) tentatively referred this species to his new genus *Paleoanculosa*, which Parodiz classified in the Pleuroceridae (Cerithioidea); subsequently, Parras & Griffin (2013: 203) concluded: “However, the simple shell of pleurocerids and *Paleoanculosa* are so generalized and devoid of distinctive features that they may easily be mistaken for shells of other unrelated groups if soft anatomy is not available. Because of this, the inclusion of *Paleoanculosa* in Pleuroceridae is unwarranted.”

*gilva*, *Natica* – Philippi, 1851b: 47–48; 1853c: 138–139, pl. 19, fig. 11. Southern China; Hohenacker. *Lunatia gilva* (Philippi, 1851) (Qi, 2004: 65, pl. 37E). Torigoe & Inaba (2011: 12–13, pl. 1, fig. 3), listed this as a junior synonym of *Laguncula pulchella* Benson, 1842, which is now classified in the Viviparidae (e.g., Richter, 2015: 11).

*remossii*, *Paludina* – Philippi, 1846w: 134 [8], pl. 2, fig. 3, ex Benson ms. Maywar, Bengal. Reeve (1863d: pl. 6, fig. 35) stated that Benson told him that Philippi’s species name was an error for *P. praemorsa*, which was the manuscript name used by Benson. Hanley & Theobald (1873: 33) rejected Reeve’s action, which would now be considered an unjustified emendation, ICZN Code Article 32.2.3, because it does not satisfy the criteria of ICZN Code Articles 32.5.1 or 33.2.3.1 (1999). *Viviparus remossi* (Philippi, 1846) (Prashad, 1928: 163), or synonym of *Idiopoma dissimilis* (O. F. Müller, 1774) (Brandt, 1974: 36–37, pl. 2, figs. 37–39).

*tenuis*, *Natica* – Philippi, 1852c: 97; 1851f: pl. 14, fig. 3, non Récluz, 1850. Mouth of the Yang-“Kwing”, China; Cécille, via Largilliert. The uncaptioned plate (1851) appeared one year before the text (1852) making the name available. From the description and illustration, it appears to be a freshwater *Viviparus* that washed down a river to the ocean. Torigoe & Inaba (2011: 12–13, pl.

1, fig. 3), listed this as a junior synonym of *Laguncula pulchella* Benson, 1842, which is now classified in the Viviparidae (e.g. Richter, 2015: 11).

### Cerithiidae

*antarcticum*, *Cerithium* – Philippi, 1858b: 23.

Strait of Magellan, Chile; George Schythe.

*armatum*, *Cerithium* – Philippi, 1848c: 22; 1849d: 16 [4], pl. 1, fig. 10, non Goldfuss, 1844. Locality unknown. Lectotype, MNHNS (no number), designated by Houbriick (1992: 103, fig. 71-A; type locality “herein designated as Marinduque Id., Philippines”) (not found in March 2014). Synonym of the western Pacific *Cerithium* (*Cerithium*) *lifuense* Melvill & Standen, 1895 (Houbriick, 1992: 103–107; Higo et al., 1999: 79).

*attenuatum*, *Cerithium* – Philippi, 1848c: 21; 1849d: 13 [1], pl. 1, fig. 2, non Forbes, 1845. Philippine Islands?”. Synonym of *Rhinoclavis* (*Longicerithium*) *longicaudata* (A. Adams & Reeve, 1850), the type species of *Longicerithium* Houbriick, 1978; type locality restricted to Pasacao, Luzon, Philippines (Houbriick, 1978b: 85–88, pls. 58–61 Higo et al., 1999: 83).

*balteatum*, *Cerithium* – Philippi, 1848c: 22–23; 1849d: 16 [4], pl. 1, fig. 8. Locality unknown. USNM 695399, neotype, designated by Houbriick (1992: 31, fig. 17-B), from Georgia Cove, Rambi Id., Vanua Levu, Fiji. The western Pacific *Cerithium* (*Ptychocerithium*) *balteatum* Philippi, 1848 (Houbriick, 1992: 31–37, figs. 17–20; Wilson, 1993: 116, pl. 17, fig. 9a, b; Higo et al., 1999: 81; Okutani, 2000: 114–115, fig. 11).

*calabrum*, *Cerithium* – Philippi, 1844g: 163; 302, pl. 25, fig. 22. Santa Severina, Calabria, Italy; fossil. *Cerithium calabrum* Philippi, 1844 (Cecalupo, 2006: 42, pl. 47, fig. 9).

*cecilli*, *Cerithium* – Philippi, 1849r: 23. Liewkiew Island, China [Ryukyu Islands, Japan]; Largilliert. Listed without discussion by Kobelt (1898: 283) and Cecalupo (2006: 186).

*dialeucum*, *Cerithium* – Philippi, 1849d: 14–15 [2–3], pl. 1, fig. 5. Locality unknown. The western Pacific and Indian Ocean *Cerithium dialeucum* Philippi, 1849 (Abbott & Dance, 1982: 65; Houbriick, 1992: 70–77, figs. 45–50; Wilson, 1993: 117, pl. 17, fig. 2; Higo et al., 1999: 79; Okutani, 2000: 114–115, fig. 6). USNM 862619, neotype, designated by Houbriick (1992: 70, fig. 46-A), from Mathuata Id., Viti Levu, Fiji.



*diminutivum*, *Cerithium* – Philippi, 1845i: 67; 1849d: 19 [7], pl. 1, fig. 17. Insulae Amicorum [Tonga]. *Cerithium diminutivum* Philippi, 1845 (Tryon, 1887a: 138, pl. 26, fig. 77); *Bittium diminutivum* (Philippi, 1845) (Cecalupo, 2006: 196).

*exiguum*, *Cerithium* – Philippi, 1845i: 67. Insulae Amicorum [Tonga]. Senior homonym of *C. exiguum* C.B. Adams, 1850, now placed in *Ataxocerithium* (Cecalupo, 2006: 200).

*filosum*, *Cerithium* – Philippi, 1849h: 143–144 (March), *non* Gould, 1849 (May), *non* G. B. Sowerby II, 1865. California; Largilliert. Gould's species is now considered to be a junior synonym of the well-known *Bittium eschrichtii* (Middendorff, 1849), which occurs from Alaska to California (Bartsch, 1911: 383); Philippi's species does not appear to have been discussed subsequently. Listed without discussion by Kobelt (1898: 280) and Cecalupo (2006: 68, 201).

*glabratum*, *Cerithium* – Philippi, 1851b: 66. Australia "?". Listed without discussion by Kobelt (1898: 284) and Cecalupo (2006: 74, 204).

*gracilum*, *Cerithium vulgatum* – Philippi, 1836a: 193, pl. 11, fig. 5, as "var.  $\epsilon$  [epsilon] *gracilis*". Mediterranean. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1884: 200), as *Cerithium vulgatum* var. *gracilis*. Syntype, ZMB 2797 (Sicily) (39.6 mm x 12.3 mm). *Cerithium gracilum* Philippi, 1836 (Kantor & Sysoev, 2005: 44; Cecalupo, 2006: 75–76, both as "*gracilis*").

*guinaicum*, *Cerithium* – Philippi, 1849d: 17–18 [5–6], pl. 1, fig. 13. Gabon; Largilliert. Type material not found; lectotype, specimen figured by Philippi, designated by Houbbrick (1974: 67). The amphi-Atlantic *Cerithium* (*Theridium*) *guinaicum* Philippi, 1849 (Houbbrick, 1974; Abbott & Dance, 1982: 66).

*kochi*, *Cerithium* – Philippi, 1848c: 21; 1849d: 14 [2], pl. 1, fig. 3. Locality unknown. Type locality restricted to Zanzibar, Tanzania; lectotype, NHMUK 1923.7.13.14 (36.2 mm x 10.4 mm) (designated by Houbbrick, 1978b: 73–79, pls. 42, fig. 1, 2, 43–47); paralectotype, NHMUK 1923.7.13.15 (32.3 mm x 9.9 mm); "another paralectotype in Chile" (not found in March 2014). The western Pacific *Rhinoclavis* (*Proclava*) *kochi* (Philippi, 1848); introduced into the Mediterranean (Abbott & Dance, 1982: 66; Sabelli et al., 1990: 136; Wilson, 1993: 124, pl. 16, fig. 11a, b; Higo et al., 1999: 83; Okutani, 2000: 122–123, fig. 44; Qi, 2004: 41, pl. 18A).

*lacteum*, *Cerithium* – Philippi, 1836a: xii, 195; 1844g: 162, 164. Ognina, Catania, Sicily, Italy. Also fossil. Syntypes, SMF 304829 (n = 4, Sicily); SMF 342262 (n = 13). *Bittium lacteum* (Philippi, 1836) (Priolo, 1956b: 253–254 [293–294]; Verduin, 1976b; Linden & Wagner, 1990, fig. 3; Sabelli et al., 1990: 142; Landau et al., 2004: 10–12, pl. 2, fig. 2). Type species (M) of *Inobittium* Monterosato, 1917, which is regarded as a synonym of *Bittium* Leach, 1847.

*laevigatum*, *Cerithium* – Philippi, 1844g: 161–162, 302, pl. 25, fig. 32 [not cited in text], *non* Serres, 1827, *non* Eichwald, 1830. Sicily, Italy. Synonym of *Potamides* (*Lampanella*) *minimus* (Gmelin, 1791) [Battilariidae] (Tryon, 1887a: 168), or of *Cerithium brongniarti* Maravigna, 1840 (Priolo, 1956b: 246 [286]); however, Maravigna's name is itself a junior homonym of *C. brongniarti* Deshayes, 1831. Cecalupo (2006: 40–41, 87) noted the multiple homonymy but did not resolve it.

*minutum*, *Cerithium vulgatum* – Philippi, 1836a: 193, pl. 11, fig. 8, as "*minuta*". Sicily, Italy. Synonym of *Cerithium vulgatum* Bruguière, 1792 (Tryon, 1887a: 126).

*nebulosum*, *Cerithium* – Philippi, 1851b: 66. Liew-Kiew Island, China [Ryukyu Islands, Japan]; Cécile via Largilliert. Listed but not discussed by Kobelt (1898: 283); incorrectly attributed to "G. B. Sowerby II, 1855" by Cecalupo (2006: 110).

*nigrinum*, *Cerithium* – Philippi, 1848c: 24; 1849d: 20 [8], pl. 1, fig. 19. Locality unknown. Type material not found; lectotype, specimen figured by Philippi, designated by Houbbrick (1974: 71, 73). Synonym of the western Atlantic *Cerithium* (*Theridium*) *lutosum* Menke, 1828.

*nodulosum*, *Cerithium vulgatum* – Philippi, 1836a: 193, pl. 11, fig. 4, as "var.  $\gamma$  [gamma] *nodulosa*", *non* *C. nodulosum* Bruguière, 1792 (Indian Ocean). Sicily, Italy. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1884: 200), as *C. vulgatum* var. *nodulosa*. Cecalupo (2006: 113) as a variety of *C. vulgatum*, but renaming would be required to avoid the homonymy. Kantor & Sysoev (2005: 44–45) listed this as a synonym of "*Cerithium spinosum*" Philippi, 1836, but that is not an available name (q.v.).

*plicatum*, *Cerithium vulgatum* – Philippi, 1836a: 193, as "*plicata*", *non* Bruguière, 1792. Sicily, Italy. *Cerithium vulgatum* var. *alucaster*



- Brocchi, 1814 (Tryon, 1887a: 126; Cecalupo, 2006: 126–127).
- pulchellum*, *Cerithium vulgatum* – Philippi, 1836a: 193, pl. 11, fig. 9, as “var.  $\eta$  [eta] *pulchella*”, non *C. pulchellum* J. De C. Sowerby, 1832. Sicily, Italy. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1884: 201), as *C. vulgatum* var. *pulchella*. Lectotype, ZMB 2790a (15.5 mm), designated by Gofas et al. (2004: 100, fig. 5), who stated that there was one other specimen in this lot that “probably does not belong to the same species” – however, there are actually 5 other specimens (not just 1) in ZMB 2790b (Kabat, pers. obs., Sept. 2013). Philippi’s subspecies was renamed *Cerithium renovatum* Monterosato, 1884. Synonym of *Cerithium repestre* Risso, 1826 (Sabelli et al., 1990: 142; Cecalupo, 2006: 129–130).
- pulicarium*, *Cerithium* – Philippi, 1848c: 20; 1849d: 6 [18], pl. 1, fig. 14. Yucatan. Synonym of *Cerithium eburneum* Bruguière, 1792 (Tryon, 1887a: 129, pl. 22, fig. 77a; Houbriick, 1974: 62).
- pumilum*, *Cerithium* – Philippi, 1851b: 66–67. Locality unknown. Listed but not discussed by Kobelt (1898: 284).
- ravidum*, *Cerithium* – Philippi, 1849d: 15–16 [3–4], pl. 1, fig. 8. Locality unknown. Type not found; *nomen dubium* and the “earliest available name” for this taxon is *C. rostratum* G. B. Sowerby II, 1855 (Houbriick, 1992: 158; Cecalupo, 2006: 134).
- rueppelli*, *Cerithium* – Philippi, 1848c: 22; 1849d: 14 [2], pl. 1, fig. 1, as *C. rüppelli*. Red Sea. Although the species name is in error, since it was based on the collector Eduard Rüppel (not “Rüppell”), ICZN Code Article 32.5.1 (1999) does not allow for a spelling correction or renaming; however, ICZN Code Article 32.5.2.1 requires correcting of the umlaut. Neotype, MNHN Paris (Suez, Egypt) (designated by Houbriick, 1992). The Red Sea *Cerithium rueppelli* Philippi, 1848 (Issel, 1869: 146, 275, as “*C. ruppelli*”; Abbott & Dance, 1982: 65, as “*C. ruppelli*” Philippi, 1849”; Houbriick, 1992: 164–168, figs. 118–121, as “*C. ruppelli*”).
- scabridum*, *Cerithium* – Philippi, 1848c: 23; 1849d: 17 [5], pl. 1, fig. 12. Red Sea; Hemprich, Ehrenberg, Rüppell. Type not found (Houbriick, 1992); Neotype, USNM 862606 (designated by Houbriick, 1992: 172, fig. 125-A), from Aden, Yemen. However, syntypes were found in 2013: SMF 228166 (n = 1) (21.8 mm x 9.0 mm); SMF 228167 (n = 1) (23.0 mm x 7.9 mm; specimen figured by Philippi?), and ICZN Code Article 75.8 (1999) applies, so that the syntypes take precedence over the neotype. The Red Sea *Cerithium scabridum* Philippi, 1848 (Houbriick, 1992: 172–177, figs. 125–128; Sabelli et al., 1990: 142). This species was introduced in the Mediterranean and is now widespread in the eastern and central parts (Zenetos et al., 2009). Type species (M) of *Bakka* Pallary, 1938, which, however, is unavailable because there was no diagnosis.
- spadiceum*, *Cerithium* – Philippi, 1851b: 67–68. Yucatan; Largilliert. *Cerithium lutosum* Menke, 1828 (Cecalupo, 2006: 148–149).
- spinosum*, *Cerithium vulgatum* – Philippi, 1836a: 193, pl. 11, fig. 3, as “var.  $\alpha$  [alpha] *spinosa*”, non *C. spinosum* Bruguière, 1792. Sicily, Italy. It does not appear that this was ever adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999). Bucquoy et al. (1884: 200) referred to “*spinosa* Blainville” and stated that it was “non Philippi,” but did not use Philippi’s name as valid. However, Blainville (1826: pl. 6A, fig. 3) used “*Cérite gommier* var. *épineuse*” as a vernacular name on a plate caption for what is now known as *Cerithium vulgatum*, and it is not an available Latin name from Blainville; it appears that “*spinosa* Blainville” was first made available by Bucquoy et al. (1884: 200). Nonetheless, Philippi’s “*spinosa*” was never adopted as an available name, so it cannot be used today. Kantor & Sysoev (2005: 44–45) used “*Cerithium spinosum* Philippi, 1836,” incorrectly as a valid species, with *C. nodulosa* Philippi, 1836, and *C. tuberculata* Philippi, 1836, as junior synonyms; further analysis is required as both *C. nodulosa* and *C. tuberculata* are junior homonyms.
- suturale*, *Cerithium* – Philippi, 1849d: 14 [2], pl. 1, fig. 4, non Risso, 1826, non Buvignier, 1843. Locality unknown. Type not found; synonym of *Cerithium dialeucum* Philippi, 1849 (Houbriick, 1992: 70; Higo et al., 1999: 79) (q.v.).
- tuberculatum*, *Cerithium vulgatum* – Philippi, 1836a: 193, pl. 11, fig. 6 [not cited in text], as “var.  $\beta$  *tuberculata*”, non *C. tuberculatum* (Linnaeus, 1758), from the Indian Ocean (now in *Clypeomorus*), non *C. tuberculatum* Blainville, 1827. Sicily, Italy. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1884: 200), as *C. vulgatum* var. *tuber-*



*culata*, but renaming would be required to avoid the homonymy. Lectotype, specimen figured by Buonanni (1684: fig. 82) as cited by Philippi, designated by Gofas et al. (2004: 100–101, fig. 6). Kantor & Sysoev (2005: 44–45) listed this as a synonym of *Cerithium spinosum* Philippi, 1836, but that is not an available name.

*versicolor*, *Cerithium* – Philippi, 1848c: 20–21. Locality unknown. Listed but not discussed by Cecalupo (2006: 166).

#### Dialidae

*semistriata*, *Rissoa* – Philippi, 1849t: 34–35. Red Sea, Aden; Th. Philippi, Hemprich & Ehrenberg; Suez, etc. Ponder & de Keyser (1992: 1022–1038) noted that the type material was lost, but that this species was based in part on the figures in Savigny (1817, pl. 3, figs. 27.1, 27.2), and that it is a senior synonym of *Diala varia* A. Adams, 1861, the type species of *Diala*. The Indo-Pacific *Diala semistriata* (Philippi, 1849) (Sabelli et al., 1990: 143; Bosch et al., 1995: 54, fig. 176; Okutani, 2000: 124–125, fig. 1; Beu, 2004: 205–206, fig. 22A–C; Severns, 2011: 72–73, figs. 2, 3); recently introduced into the Mediterranean.

#### Diastomatidae

*cerithina*, *Rissoa* – Philippi, 1849t: 33–34. Red Sea, Aden; Th. Philippi. *Clathrofenella cerithina* (Philippi, 1849), Indo-Pacific; introduced into the Mediterranean (Janssen et al., 2011: 398–399, pl. 7, figs. 3–7).

#### Litiopidae

*virgata*, *Rissoa* – Philippi, 1849t: 35. Red Sea, Aden; also cited Savigny, 1809: pl. 3, fig. 29; Th. Philippi, Hemprich & Ehrenberg; Suez, etc. Lectotype, MNHN Paris (from Egypt), designated by Aartsen (2002: 57–58, fig. 1); paralectotypes (n = 3), MNHN Paris. Now classified in the Litiopidae, *Gibborissoa virgata* (Philippi, 1849) (Bosch et al., 1995: 55, fig. 178; Swennen et al., 2001: 52, fig. 289, both as *Alaba*; Aartsen, 2002), and introduced into the Mediterranean (Aartsen, 2002).

#### Melanopsidae

*kotschyi*, *Melania* (*Melanopsis*) – Philippi, 1847d: 175–176 [25–26], pl. 4, fig. 11.

Persepolis [Persia, now Iran]; Kotchy. This species was credited to Busch by Sherborn (1927: 3325), but the description was signed by Philippi.

*parreyssii*, *Melania* (*Melanopsis*) – Philippi, 1847d: 176 [26], pl. 4, fig. 15, ex Megerle von Mühlfeld ms. Hungary; Parreyss. This species was credited to Megerle von Mühlfeld by Sherborn (1929: 4766), but the description was signed by Philippi. *Melanopsis parreysii* (Philippi, 1847) (Glöer, 2002: 76), or as *Microcolpia parreysii* (Philippi, 1847) (Neubauer et al., 2014). Type species (M) of *Parreyssiana* Bourguignat, 1884, a synonym of *Melanopsis* A. Férussac, 1807.

*variabilis*, *Melania* (*Melanopsis*) – Philippi, 1847d: 175 [25], pl. 4, figs. 7, 8, 10, ex Busch ms, *non* Defrance, 1823, *non* Benson, 1836, *non* Klepstein, 1845. Schiraz & Persepolis [Persia, now Iran]. This species was credited to Busch by Sherborn (1931: 6796), but it was unsigned and seems to be parallel to *Melania kotschyi*, which was signed by Philippi. *Melanopsis variabilis* (Philippi, 1847) (Kantor & Sysoev, 2005: 47, as “Busch in Philippi”), but unfortunately Philippi’s name is a junior homonym three times over.

#### Modulidae

*catenulatus*, *Trochus* – Philippi, 1849z3: 110; 1847z5: pl. 18, fig. 4. Locality not indicated. The uncaptioned plate (1847) appeared two years before the text (1849) making the name available. The Panamic *Modulus catenulatus* (Philippi, 1849) (Keen, 1971: 399–400, fig. 490; Abbott & Dance, 1982: 63; Ramírez et al., 2003: 259). Type species (OD) of *Trochomodulus* Landau et al., 2014: 7.

*disculus*, *Trochus* – Philippi, 1846h: 51–52; 1849z3: pl. 36, fig. 14; 1852d: 242–243. Mazatlán, Sinaloa, Mexico. The Panamic *Modulus disculus* (Philippi, 1846) (Keen, 1971: 399–400, fig. 492; Abbott & Dance, 1982: 63).

#### Pachychilidae

*angusta*, *Melania* – Philippi, 1848e: 57 [31], pl. 5, fig. 9. Locality unknown; Pfeiffer.

*araucana*, *Melania* – Philippi, 1887a: 80 [1887b: 75], pl. 9, fig. 11. Puchoco, Chile; Volckmann; Tertiary. Syntypes, SGO.PI.758 (labeled as “lectotipo”); SGO.PI.4655–4660 (labeled as “paralectotipo”).

*balteata*, *Melania* – Philippi, 1851a: [4]. Replacement name for *M. zonata* Philippi, 1848,



- non* Busch, 1843. Synonym of *Pachymelania aurita* (O. F. Müller, 1774), from tropical western Africa (Smith, 1893: 142).
- belone*, *Melania* – Philippi, 1851c: 81. Locality unknown; Bernardi.
- bensoni*, *Melania* – Philippi, 1851c: 82. Locality unknown.
- cecillii*, *Melania* (*Pirena*) – Philippi, 1849s: 28. Madagascar. Köhler & Glaubrecht (2010: 873) rejected attempts by earlier authors, such as that by Starmühlner (1969: 159–182), to synonymize this species with “*Melanatria fluminea* (Gmelin, 1791)” [now *Madagasikara spinosa* (Lamarck 1822)], concluding that “Because the whereabouts of the [Philippi’s] types are unclear, the status ... remains unclear.”
- coffea*, *Melania* – Philippi, 1843j: 60 [8], pl. 2, fig. 4. “Java?”.
- divisa*, *Melania* – Philippi, 1851c: 81–82. Locality unknown.
- fontinalis*, *Melania* – Philippi, 1848e: 57–58 [31–32], pl. 5, fig. 7. Pulo Pinang; Th. Philippi. Syntypes, SMF 302375 (n = 4) (largest, 10.3 mm x 4.4 mm).
- hohenackeri*, *Melania* – Philippi, 1851c: 82–83. Mountain rivers, Surinam; Hohenacker. *Dorissa hohenackeri* (Philippi, 1851) (Simone, 2006: 73, fig. 161).
- huegelii*, *Melania* – Philippi, 1843j: 61–62 [9–10], pl. 2, fig. 8, as “*Hügelii*”. “New Holland?” [Australia]. In a footnote, Philippi said that Parreyss had intended to call the species *breviformis*, a name that Philippi declined to use. Holotype, MNHNS (Köhler & Glaubrecht, 2007: 632, fig. 1-A) (not found in March 2014); the two possible syntypes (ZMB 200161) identified by Köhler & Glaubrecht (2002: 138–139) are not type material as the species was based on a single specimen. Type species (SD Brot, 1879) of *Acrostoma* Brot, 1871, *non* Le Sauvage, 1827 [Platyhelminthes], *non* Grube, 1840 [Polychaeta]. *Brotella* Rovereto, 1899, *nom. nov. pro Acrostoma* Brot, 1871, but itself *non Brotella* Kaup, 1858 [Pisces]. *Paracrostoma* Cossmann, 1900, *nom. nov. pro Acrostoma* Brot, 1871, and *Brotella* Rovereto, 1899. *Paracrostoma huegelii* (Philippi, 1843), from southern India (Köhler & Glaubrecht, 2007: 631–638).
- humilis*, *Melania* – Philippi, 1851c: 82. Locality unknown.
- inhonesta*, *Melania* – Philippi, 1847d: 170–171 [20–21], pl. 4, fig. 5, ex Busch ms. Java “?”.
- largillierti*, *Melania* – Philippi, 1843j: 62 [10], pl. 2, fig. 10. Central America. Syntypes ZMB 112.944 (n = 1); ZMB 112.945 (n = 3) (Gomez-Berning et al., 2012: 19–20, fig. 3H); SMF 302370 (n = 3) (“Guatemala”). *Pachychilus* (*Glyptomelania*) *largillierti* (Philippi, 1843), from Guatemala, Nicaragua and El Salvador (Thompson, 2011: 39).
- liebmanni*, *Melania* – Philippi, 1848e: 58 [32], pl. 5, fig. 8. Mexico; Liebmann. Types probably lost (Gomez-Berning et al., 2012: 20). Type species (OD) of *Cercimelania* Crosse & Fischer, 1892. *Pachychilus* (*P.*) *liebmanni* (Philippi, 1848), from Veracruz, Mexico (Thompson, 2011: 36).
- obesa*, *Melania* “?” – Philippi, 1847d: 170 [20], pl. 4, fig. 3. Australia “?”.
- petiti*, *Melania* – Philippi, 1849i: 153–154. New Caledonia. *Melania petiti* Reeve, 1859: pl. 9, fig. 47, ex Philippi ms. is a junior homonym of *M. petiti* Philippi, 1849; Reeve’s species was renamed *Melania sulcatina* Brot, 1877.
- picta*, *Melania* – Philippi, 1849i: 154. Manila, Philippine Islands; Largilliert.
- pugioniformis*, *Melania* – Philippi, 1851c: 83. Locality unknown.
- rivularis*, *Melania* – Philippi, 1847d: 171 [21], pl. 4, fig. 6. Java; Dupuy. Synonym of *Melanoides tuberculata* (O. F. Müller, 1774) (Brandt, 1974: 165).
- scabrella*, *Melania* – Philippi, 1847d: 172 [22], pl. 4, fig. 13. Java.
- schiedeana*, *Melania* – Philippi, 1843j: 62–63 [10–11], pl. 2, fig. 11. Rivuli, Mexico; Schiede. ZMB 112.952a, lectotype (22.0 mm x 8.8 mm) (designated by Gomez-Berning et al., 2012: 35, fig. 7A); ZMB 112.952b, paralectotype. Type species (OD) of *Oxymelania* Crosse & P. Fischer, 1892. *Pachychilus* (*Oxymelania*) *schiedeanus* (Philippi, 1843), from Veracruz, Mexico (Thompson, 2011: 41).
- semicostata*, *Melania* – Philippi, 1847d: 171–172 [21–22], pl. 4, fig. 12. Java; Dupuy. Synonym of *Sermyla riqueti* (Grateloup, 1840) (Brandt, 1974: 169, pl. 12, figs. 19–22).
- sinuosa*, *Pirena* – Philippi, 1851c: 91. Nossibè, Madagascar. Köhler & Glaubrecht (2010: 873) rejected the attempts by Starmühlner (1969: 159–182) and Fischer-Piette & Vukadinovic, 1973: 356–359) to synonymize this species with “*Melanatria fluminea* (Gmelin, 1791)” [now *Madagasikara spinosa* (Lamarck 1822)], concluding that “Because the whereabouts of the [Philippi’s] types are unclear, the status ... remains unclear.”
- soluta*, *Melania* “?” – Philippi, 1844g: 121, 301, as “*M. sulcata*”, pl. 24, fig. 1. Santa Severina, Crotone, Calabria, Italy; fossil.



- spacidea, Melania* – Philippi, 1849i: 154. Manila, Philippine Islands.
- subimbricata, Melania* – Philippi, 1848e: 56 [30], pl. 5, fig. 3. Locality unknown; Koch.
- subnodosa, Melania* – Philippi, 1847d: 173–174 [23–24], pl. 4, fig. 18. Central America. Type material not found (Gomez-Berning et al., 2012: 38). *Pachychilus (Glyptomelania) subnodosus* (Philippi, 1847), from Nicaragua (Thompson, 2011: 39).
- sulcata, Melania* – Philippi, 1844g: 301. Error for *Melania soluta* Philippi, 1844.
- suturalis, Melania* – Philippi, 1847d: 173 [23], pl. 4, fig. 17. Locality unknown. Synonym of *Melanoides tuberculata* (O. F. Müller, 1774), southeast Asia (Brandt, 1974: 165).
- tugidula, Melania* – Philippi, 1847d: 171 [21], pl. 4, fig. 9. “China? Manila?”.
- villosa, Melania* – Philippi, 1849i: 154. Locality unknown. Treated by Gassies (1863: 295 [repr. p. 91], pl. 4, fig. 7), as being from New Caledonia. Erroneously indicated by Ruhoff (1980: 565) as being by “Philippi, in Gassies, 1863”.
- zonata, Melania* – Philippi, 1848e: 57 [31], pl. 5, fig. 5, *non* Busch, 1842. Locality unknown; Pfeiffer. Renamed *Melania balteata* Philippi, 1851 (q.v.).

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- “*atra, Melania*” – Philippi, 1848e: 55 [29]. Listed by some authors as a Philippi species, such as Simone (2006: 70), this was first made available as *Bulimus atra* Bruguière, 1792, now *Doryssa atra* (Bruguière, 1792).
- “*potius, Melania*” – Menke, 1844: 15, ex Philippi ms. This species name, attributed by Menke to Philippi, was listed by Menke as a synonym of *Melania philippi* Dunker, 1843, a fossil from Germany.
- “*turritella, Melania*” – Sherborn (1931: 6696) erroneously listed this species as of Philippi, but the article involved was by Dunker (1846: 169), without any species attributed to Philippi. Dunker’s species was *non* Nyst, 1836, *non* Pfeiffer, 1840.
- “*zinkenii, Melania*” – Sherborn (1932: 7045) erroneously listed this species as of Philippi, but the article involved was by Dunker (1846: 169), without any species attributed to Philippi.

## Planaxidae

- Fossarus* – Philippi, 1841a: 42–47, 59. Type species (M): *Fossarus adansoni* Philippi,

1841, = *Turbo ambiguus* Linnaeus, 1767. Valid genus of the Fossarinae. Monterosato (1884a: 110; 1884b: 52) thought that *Maravignia* Aradas & Maggiore, “1840”, had priority over *Fossarus*, but *Maravignia* was not actually published until 1844, and its type species is a “deformed specimen” of *F. ambiguus*, so that the generic names are synonyms (Bouchet & Warén, 1988: 86).

- adansonii, Fossarus* – Philippi, 1841a: 47, 59, pl. 5, fig. 1; 1844g: 147–148, 302, pl. 25, fig. 1, 1a. Species based on Adanson’s pre-Linnean description, Scacchi’s material and Philippi’s own material. Eastern Atlantic. Possible syntypes, SMF 305109 (n = 2) (Naples, ex Philippi). Synonym of *Fossarus ambiguus* (Linnaeus, 1758) (Priolo, 1961: 86–88 [426–428]; Sabelli et al., 1990: 143, as *F. adansoni*).
- incisus, Planaxis* – Philippi, 1851c: 92. Locality unknown.
- piliger, Planaxis* – Philippi, 1849i: 164–165. Bourbon Island; Largilliert. Syntypes, Muséum de Rouen 168001040 (n = 5) (largest, 8.4 mm x 5.6 mm); MNHN Paris (n = 2) (8.3 mm x 6.1 mm; 8.2 mm x 5.9 mm). Type species (M) of *Holcostoma* H. Adams & A. Adams, 1854.
- striatulus, Planaxis* – Philippi, 1851c: 91–92. Locality unknown. Perhaps a senior synonym of the western Pacific *Angiola zonata* (A. Adams, 1853). Listing mixed up in Higo et al. (1999: 77) as “*P. striatulus* Philippi, Martens & Langkavel, 1871.”
- taeniatus, Planaxis* – Philippi, 1849i: 165–166. Locality unknown.

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- “*costata, Adeorbis*” – Clench, 1975: 31 cited this as a Philippi, 1844, species, and a senior homonym of *Adeorbis costata* Garrett, 1857. However, Philippi did not use the genus *Adeorbis*, and Philippi’s usage was of *Delphinula costata* (Brocchi, 1814) (described in *Turbo*), *non* Gmelin, 1791. Philippi (1844: 147, 278) treated Brocchi’s name (which he attributed to Bronn, 1831) as a synonym of *Fossarus adansoni* Philippi, 1844. In contrast, Sabelli et al. (1990: 222) listed *costata* Brocchi *non* Gmelin as a synonym of *Clathrella clathrata* (Philippi, 1844), which is now in the Amathinidae.

## Potamididae

- alatum, Cerithium* – Philippi, 1849d: 17 [5], pl. 1, fig. 11. Mergui Archipelago, Burma



[Myanmar]; Th. Philippi. *Cerithidea* (*Cerithideopsis*) *alatum* (Philippi, 1849), central Indo-West Pacific (Altena, 1940: 218–220; Brandt, 1974: 191, pl. 14, fig. 50).

*carbonarium*, *Cerithium* – Philippi, 1849h: 142, China; Largilliert. Synonym of *Batillaria sordida* (Gmelin, 1791) (Houbrick, 1978a: 643, 645).

*hegewischii*, *Cerithium* (*Potamides*) – Philippi, 1848c: 19; 1849d: 13 [3], pl. 1, fig. 6. Mexico; Hegewisch. Synonym of *Cerithidea montagnei* (d'Orbigny, 1839), tropical eastern Pacific (Tryon, 1887a: 161). However, Keen (1971: 419) stated that references to Philippi's name in the eastern Pacific literature were doubtful, and were better assigned to *C. mazatlanica* Carpenter, 1857, a conclusion followed by Cecalupo (2006: 78–79).

*largillierti*, *Cerithium* (*Potamides*) – Philippi, 1848c: 20; 1849d: 15 [3], pl. 1, fig. 6. China; Largilliert. Neotype, NHMUK 20130431 (Shanghai) (designated by Reid & Claremont, 2014: 68–71, figs. 2A–E, 3A, 4). Frequently and erroneously classified as *Cerithidea largillierti* (Philippi, 1848) (Wilson, 1993: 133, pl. 15, fig. 12; Higo et al., 1999: 87; Okutani, 2000: 132–133, fig. 3; Qi, 2004: 38, pl. 16E), but it is an Indo-Pacific species *Cerithideopsis* (Reid, 2014: 8).

*sinense*, *Cerithium* (*Potamides*) – Philippi, 1848c: 19–20; 1849d: 18 [6], pl. 1, fig. 15. China; Largilliert. Syntypes, MNHN Paris 25694 (n = 2) (27.9 mm x 11.9 mm; 18.5 mm x 7.6 mm); Muséum de Rouen 168001041 (n = 14) (largest 26.3 mm x 10.4 mm). *Cerithidea sinensis* (Philippi, 1848) (Qi, 2004: 38, pl. 16D; Reid, 2014: 23–25, figs. 6, 7A–L).

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“*mamillata*, *Potamides* (*Pirenella*)” – Fischer (1887: 681) cited this as a Philippi species, but it is a misidentification (and misspelling) of *Cerithium mammillatum* Risso, 1826, by Philippi (1836a: 194), not a new species. Philippi's material is referable to *Pirenella conica* (Blainville, 1829) (Priolo, 1956b: 233 [273]), while Risso's species is now in *Bittium*.

#### Scaliolidae

*secalina*, *Melania* – Philippi, 1841f: 19–20; 1844z4: 19–20, [87], pl. 3, fig. 15. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Sandbergeria secalina* (Philippi, 1841) (Speyer, 1869: 300–301, pl. 31, figs.

3–6; Anderson, 1960a: 63, pl. 11, figs. 3, 3a; Janssen, 1978a: 54, 1978b: 164, pl. 11, fig. 38, both of whom dated the species from 1843). Type material lost (R. Janssen, pers. comm., April 2013).

#### Turritellidae

*angusta*, *Turritella* – Philippi, 1887a: 78 [1887b: 73], pl. 9, fig. 5. Puchoco, Chile; Tertiary. Holotype, SGO.PI.609.

*darwini*, *Turritella* – Philippi, 1887a: 75 [1887b: 70], pl. 9, fig. 7. Navidad, Lota, Tubul & Lebu “?”, Chile; Tertiary. Syntypes, SGO.PI.679 (n = 6, Navidad); SGO.PI.607 (n = 11, Tubul); SGO.PI.676 (n = 2, Lebu).

*elegans*, *Turritella* – Philippi, 1887a: 76 [1887b: 71], pl. 9, fig. 3, *non* Deshayes, 1861. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.672.

*landbecki*, *Turritella* – Philippi, 1887a: 75 [1887b: 70], pl. 9, fig. 4. Algarrobo, Chile; Ludw. Landbeck; Cretaceous. Syntypes, SGO.PI.617 (labeled as “lectotipo”); SGO.PI.678 (several fragments); SGO.PI.681 (n = 6); SGO.PI.4819 (n = 1); SGO.PI.4820 (n = 1); SGO.PI.4638 (n = 2); SGO.PI.4639–4647 (n = 1 each). *Turritella landbecki* Philippi, 1887 (Tavera, 1942: 590, fig. 6; Bandel & Stinnesbeck, 2000: 762)

*leptogramma*, *Turritella* – Philippi, 1887a: 75 [1887b: 70], “pl. 9, fig. 30” [but not on plate]. Algarrobo, Chile; Cretaceous & Navidad, Chile; Tertiary. Syntypes, SGO.PI.600 (n = 2); SGO.PI.610 (n = 1); according to DeVries (2007: 335), the latter syntype “is best referred to *Incatella chilensis*”. *Incatella leptogramma* (Philippi, 1887).

*parvula*, *Turritella* – Philippi, 1887a: 78 [1887b: 73], pl. 57, fig. 4. Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.4622–4637. “Appear to be juvenile specimens” of *Incatella trilirata* (Philippi, 1887) (DeVries, 2007: 337–338, figs. 3.18, 3.19).

*quadrangulus*, *Vermetus* – Philippi, 1848c: 17. Yucatan. *Vermicularia* (Bieler & Petit, 2011: 54), probable synonym of *Vermicularia spirata* (Philippi, 1836) (Mörch, 1861: 174).

*sowerbyana*, *Turritella* – Philippi, 1887a: 76 [1887b: 71], pl. 9, fig. 2, *nom. nov. pro Turritella suturalis* G. B. Sowerby I, 1846, *non* Forbes, 1844; also *non* J. Phillips, 1836. However, *T. suturalis* had already been renamed *Turritella pseudosuturalis* d'Orbigny, 1852 (Griffin & Nielsen, 2008: 307, pl. 24, fig. 9).



*spiratus*, *Vermetus* – Philippi, 1836b: 224–225, 235 [pl. expl.], pl. 7, fig. 1. Havana, Cuba. Syntype, ZMB (Bieler & Hadfield, 1990: 219); possible syntypes, MNHN Paris (n = 6). *Vermicularia spirata* (Philippi, 1836) (Abbott & Dance, 1982: 61; Rios, 1994: 66, pl. 22, fig. 250; Tunnell et al., 2010: 136; Bieler & Petit, 2011: 60; Redfern, 2013: 39, fig. 110).

*trilirata*, *Turritella* – Philippi, 1887a: 75 [1887b: 71], pl. 9, fig. 8. Navidad & Lota, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.612 (n = 1, Navidad, labeled as “lectotipo”); SGO.PI.4617–4621 (n = 1 each, all from Navidad). *Incatella trilirata* (Philippi, 1887) (DeVries, 2007: 337–338, figs. 3.18, 3.19).

### Calyptraeidae

*araucana*, *Trochita* – Philippi, 1887a: 92–93 [1887b: 87], pl. 11, fig. 1. Lebu & Guayacán, Chile; Tertiary. Syntypes, SGO.PI.682 (labeled as “lectotipo”); SGO.PI.4711–4713 (each labeled as “paralectotipo”). Junior secondary homonym of *Trochita araucana* (Lesson, 1830); renamed *Calyptraea pueyrredona* Ihering (1907: 149) and yet again as *Calyptraea levuana* Ihering (1907: 523). Parodiz (1996: 237, 257) incorrectly stated that MACN 666 consisted of two syntypes from Lagoa Pueyrredón (Santa Cruz, Argentina), which he stated was the type locality, but these specimens are merely those collected by Hatcher and given by Ortmann to Ihering, and are not Philippi’s original type material.

*argentina*, *Brocchia* “?” – Philippi, 1893b: 7, pl. 1, fig. 9. Argentina; Tertiary. *Crucibulum argentinum* (Philippi, 1893), Miocene (Ihering, 1907: 366; Martínez et al., 1998: 33, pl. 15, figs. 1–3, pl. 23, fig. 2).

*atra*, *Crepidula* – Philippi, 1851b: 69. Locality unknown.

*colchaguensis*, *Trochita* – Philippi, 1887a: 93 [1887b: 88], pl. 11, fig. 5. La Cueva, Colchagua, Chile; Tertiary. Holotype, SGO.PI.686. *Trochita colchaguensis* Philippi, 1887, Pliocene (Nielsen, 2013: 40–41, figs. 3n–p).

*coriocella*, *Crepidula* – Philippi, 1887a: 94 [1887b: 89], pl. 11, fig. 7. Cueva de Cucao, Chile; Tertiary. “Not a calyptraeid” (Hoagland, 1977: 356).

*costellata*, *Calyptraea* – Philippi, 1845i: 62. Strait of Magellan, Chile. Syntypes, MNHNS 193 (n = 4, largest, 10.7 mm x 22.4 mm); Pastorino & Urteaga (2012: figs. 16–18) figured the “probable holotype” from the MNHNS, but apparently from another, un-numbered lot.

Synonym of *Trochita pileus* (Lamarck, 1822) (Forcelli, 2000: 74; Pastorino & Urteaga, 2012: 72–73), or a valid species of *Calyptraea* (Carcelles & Williamson, 1951: 279; Valdovinos, 1999: 133).

*costellata*, *Trochita* – Philippi, 1887a: 93 [1887b: 87–88], pl. 11, fig. 4, *non* Conrad, 1855. Lebu, Chile; Tertiary. Holotype, SGO.PI.685. Synonym of *Calyptraea pileus* var. *merriami* (Ortmann, 1899) (Ihering, 1907: 340), or of *Trochita pileus* (Lamarck, 1822) (Rehder, 1943: 44).

*decipiens*, *Calyptraea* – Philippi, 1845i: 61–62. Strait of Magellan, Chile. Syntypes, SMF 305080 (n = 3) (largest, 26.8 mm x 22.2 mm x 6.9 mm); ZMB 3330 (n = 1) (10.4 mm x 9.8 mm x 4.4 mm). Synonym of *Trochita pileolus* (d’Orbigny, 1841) (Ihering, 1907: 150; Castellanos & Landoni, 1990: 9; Pastorino & Urteaga, 2012: 70–72), or a valid species of *Trochita* (Rehder, 1943: 44; Valdovinos, 1999: 133; Letelier et al., 2003: 72).

*excisa*, *Crepidula* – Philippi, 1849r: 24. Mergui Archipelago, Burma [Myanmar]. Possible syntypes, ZMB 121032 (n = 2) (Mergui, ex Dunker and Gruner). “Nomen oblitum” and possibly the same as *C. walshi* Reeve, 1859 (Hoagland, 1977: 393).

*inperforata*, *Haliotis* “?” – Philippi, 1887a: 102–103 [1887b: 97], pl. 12, fig. 2. Skyring Water, Chile; Enrique Ibar; [Cenozoic]. Transferred to Calyptraeidae; synonym of *Crepidula gregaria* G. B. Sowerby I, 1846 (Ortmann, 1898: 479; 1902: 184).

*laevis*, *Trochita* – Philippi, 1887a: 92 [1887b: 87], pl. 11, fig. 3. Isla Quiriquina, Chile. Syntypes, SGO.PI.687 (labeled as “lectotipo”); SGO.PI.4677 (n = 1, labeled as “paralectotipo”). Griffin & Hünicken (1994: 262) concluded that this species was probably referable to *Spirogalerus* (Calyptraeidae). *Sigapatella* (*Spirogalerus*?) *laevis* (Philippi, 1887), Palaeocene (Stilwell, 2003: 352).

*mytilina*, *Crepidula* – Philippi, 1887a: 94 [1887b: 89], pl. 11, fig. 8. Lebu, Chile; Orvalle; Tertiary. Possible synonym of *C. unguiformis* Lamarck, 1822 (Hoagland, 1977: 356).

*parvula*, *Trochita* – Philippi, 1887a: 93 [1887b: 87], pl. 11, fig. 2, *non* Dunker, 1875. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.684. *Calyptraea pileus* var. *merriami* (Ortmann, 1899) (Ihering, 1907: 340).

*solida*, *Crepidula* – Philippi, 1851b: 69–70, *non* Hinds, 1844. Locality unknown.

*uncinata*, *Crepidula* – Philippi, 1887a: 94 [1887b: 88], pl. 11, fig. 6. La Cueva, Chile;



Tertiary [Pliocene]. Holotype, SGO.PI.825. Synonym of *Crepipatella dilatata* (Lamarck, 1822) (Hoagland, 1977: 372; Nielsen, 2013: 41, fig. 3s, 3t).

*vestita*, *Calyptraea* – Philippi, 1851b: 65–66. Locality unknown.

*vulgaris*, *Calyptraea* – Philippi, 1836a: x, 119; 1844g: 93. Sicily, Italy. Also fossil. Syntype, PHB MB Ga. 1841 (V) 99. Synonym of the western Atlantic *Calyptraea chinensis* (Linnaeus, 1758) (Priolo, 1963: 1–4 [437–440]; Kantor & Sysoev, 2005: 50–51). Janssen (1978a: 83–84) determined that the Oligocene specimens that Philippi (1844z4: 16) also identified as this species were also referable to *Calyptraea chinensis* (Linnaeus, 1758).

#### Capulidae

*kroeyeri*, *Trichotropis* – Philippi, 1849i: 175–176, as *T. kröyeri*. Spitzbergen; Kröyer. Syntype, ZMB 32014 (30.8 mm x 21.3 mm). The Arctic *Neoiphinoe kroeyeri* (Philippi, 1849) (Higo et al., 1999: 118; Okutani, 2000: 198–199, fig. 19; Kantor & Sysoev, 2005: 52–53, all as *N. "kroyeri"*). ICZN Code Article 32.5.2.1 (1999) requires the addition of an e to the species name. Type species (OD) of *Ovotropis* Egorov & Alexeyev, 1998, regarded as a junior synonym of *Neoiphinoe* Habe, 1978 by subsequent authors.

*papyraceus*, *Capulus* “?” – Philippi, 1887a: 95 [1887b: 89], pl. 11, fig. 9. Tucapel, near Lebu, Chile; Tertiary.

#### Cypraeidae

*caputanguis*, *Cypraea* – Philippi, 1849r: 24, as *C. caput anguis*. Locality unknown. Synonym of the Indo-Pacific *Ravitrana caputserpentis* (Linnaeus, 1758) (Wilson, 1993: 179, pl. 34, fig. 2a–c; Higo et al., 1999: 128), the type species of *Ravitrana* Iredale, 1930.

*chilensis*, *Cypraea* – Philippi, 1887a: 74 [1887b: 70], pl. 8, fig. 16. Caldera, Chile; Tertiary. *Calistocypraea* (*Miolyncina*) *chilensis* (Philippi, 1887) (Schilder, 1932: 131).

*parvula*, *Cypraea* – Philippi, 1849r: 24–25. Locality unknown. Synonym of *Bistolida hirundo* (Linnaeus, 1758), Indo-Pacific (Schilder, 1932: 131).

*sphaerica*, *Cypraea* – Philippi, 1845z: 449 [nomen nudum]; 1847-l: 79–80, pl. 10a, fig. 15. Westeregeln, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene. Synonym

of *Eocypraea* (*Sphaerocypraea*) *ovaria* (Schlotheim, 1820) (Schilder, 1932: 219).

#### Ovulidae

*Thyreus* – Philippi, 1844g: 92–93, non Panzer, 1806 [Hymenoptera]. Type species (M): *Thyreus paradoxus* Philippi, 1844, = *Pedicularia sicula* Swainson, 1840. Recent, Mediterranean. Synonym of *Pedicularia* Swainson, 1840, which has the same type species.

*paradoxus*, *Thyreus* – Philippi, 1844g: 92–93, 300, pl. 18, fig. 11a–e. Italy; Scacchi; from corals. Synonym of *Pedicularia sicula* Swainson, 1840 (Priolo, 1963: 48–59 [494–495]; Sabelli et al., 1990: 167; Bouchet & Warén, 1993: 749–752, figs. 1772–1787).

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“*Calpurinus*” – Philippi, 1853a: 442, misspelling of *Calpurnus* Monfort, 1810.

#### Ficidae

*gracilis*, *Ficula* – Philippi, 1849g: 97–98. Campeche, Mexico; Florida. Probable junior synonym of the western Atlantic *Ficus papyratia* (Say, 1822); junior secondary homonym of *Ficus gracilis* (G. B. Sowerby I, 1825).

#### Littorinidae

The original correct spelling of the type genus is *Littorina* Férussac, 1822. A number of subsequent authors spelled the name as *Litorina* starting with Menke, 1828, and including Philippi.

*Bembicium* – Philippi, 1846s: 129–133. Type species (SD Gray, 1847): *Trochus melanosoma* Gmelin, 1791. Recent, Australia. Junior objective synonym of *Risella* Gray, 1842, as noted by Philippi (1851b: 31; 1853a: 176) and by Petit (2012: 98–99). Carter (2007) incorrectly dated Gray’s taxon to 1847 instead of 1842. A petition to the ICZN is required, and ICZN Code Article 23.9 (1999) cannot be invoked in that *Risella* was used as a valid name after 1899. Although effectively a *nomen oblitum*, as Reid (1988: 116) asserted, in the absence of an ICZN ruling *Risella* remains a potentially valid name. According to the online *Zoological Record* (which indexes articles in greater detail than books), *Risella* has been used for molluscs only three times since 1952, each time as a junior synonym,



- while *Bembicium* has been used in 35 papers since 2000, and 80 papers from 1980 to the present, including numerous marine ecology and pollution studies, as well as in several books, which weighs in favor of conserving *Bembicium* over *Risella*.
- aberrans*, *Litorina* “?” – Philippi, 1846g: 142–143; 1847u: 11 [47], pl. 6, fig. 9. Panama; Cuming. Holotype, NHMUK 1968325 (ex Cuming) (16.6 mm x 10.4 mm). The Panamic *Littoraria* (*Bulimilittorina*) *aberrans* (Philippi, 1846) (Reid, 1999: 43–47, various figures). Type species (OD) of *Bulimilittorina* Reid, 1989.
- africana*, *Litorina* – Philippi, 1847i: 199 [31], pl. 4, fig. 10, ex Krauss ms. Cape of Good Hope, South Africa. Credited by Sherborn (1923: 136) to “Krauss in Philippi”; while the header indicated Krauss as the author, the description was signed by Philippi, and the name was indicated as being “in literis”, so Philippi should be regarded as its author. Sherborn also misdated this species as 1846 from Krauss’ book on South African molluscs, but the book did not appear until 1848. Lectotype, Stuttgart Museum ZI 0050275 (formerly MT 106), designated by Janus (1961: 5, pl. 3, figs. 1–2); paralectotype Stuttgart Museum ZI 0050276 (formerly MT 1060); additional type material elsewhere (Herbert & Warén, 1999: 215). This taxon is the type species (OD) of *Afrolittorina* S. Williams, Reid & Littlewood, 2003; Reid & Williams (2004: 100–102, fig. 15A, lectotype figure). Thus, *Afrolittorina africana* (Philippi, 1847).
- albida*, *Litorina* – Philippi, 1848f: 63–64 [57–58], pl. 7, fig. 9. Realtejos, Nicaragua; Petit. Possible synonym of *Echinolittorina modesta* (Philippi, 1846); types not found (Reid, 2002: 111).
- ambigua*, *Litorina* (*Phasianella*) – Philippi, 1848f: 62–63 [56–57], pl. 7, fig. 6, ex Nuttall ms. Hawaii. Lectotype, NHMUK 1968314/1 (15.7 mm x 11.6 mm) (designated by Rosewater, 1970: 447, pl. 346, figs. 3–4); paralectotype, NHMUK 1968314/2. Synonym of the Indo-Pacific *Littoraria* (*Littorinopsis*) *intermedia* (Philippi, 1846) (Reid, 1986: 124, fig. 43).
- antipodum*, *Litorina* – Philippi, 1847i: 195–196 [27–28], pl. 4, fig. 2. New Zealand; Petit. Lectotype, specimen figured by Philippi (pl. 4, fig. 2, New Zealand), designated by Reid & Williams (2004: 92–93, fig. 9D). *Austrolittorina antipodum* (Philippi 1847), New Zealand (Reid & Williams, 2004: 92–95).
- antonii*, *Litorina* – Philippi, 1846x: 145 [15], pl. 2, fig. 18. Antilles. Syntypes, NHMUK 20110266 (n = 2) (Antilles, ex Cuming, label in Philippi’s handwriting). The western Atlantic *Tectarius antonii* (Philippi, 1846) (Bandel & Kadolsky, 1982: 34–37, figs. 1D, 3C, 11, 56–59, as *Nodilittorina*; Redfern, 2013: 47, fig. 132).
- arctica*, *Lacuna* – Philippi, 1853e: 41–42, pl. 6, fig. 5. Greenland. Synonym of *Lacuna vineta* (Montagu, 1803).
- articulata*, *Litorina intermedia* – Philippi, 1846g: 141; 1847o: 223 [40], pl. 5. Swan Point, Australia; Cuming collection. Neotype, NHMUK 1968348 (designated by Reid, 1986: 200 fig. 90b) (14.3 mm x 9.6 mm). The southeast Asian and Australian *Littoraria* (*Palustorina*) *articulata* (Philippi, 1846) (Reid, 1986: 200–209, figs. 90–94, 2001: 134–135, figs. 53–55, 65–68; Wilson, 1993: 146, pl. 18, fig. 6a, b; Higo et al., 1999: 92; Okutani, 2000: 140–141, fig. 20).
- articulata*, *Litorina scabra* – Philippi, 1847o: 222 [38], pl. 5, fig. 4, *non* Philippi, 1846. Panay & Mindanao; Cuming. Lectotype, NHMUK 1968354/1 (31.7 mm x 18.4 mm) (designated by Rosewater, 1970: 459, pl. 352, fig. 6); paralectotypes NHMUK 1968354/2–4 (n = 3). Listed by Reid (1986: 124, fig. 43) and Higo et al. (1999: 92) as a synonym of *Littoraria* (*Littorinopsis*) *intermedia* (Philippi, 1846).
- aspera*, *Litorina* – Philippi, 1846g: 139; 1847i: 200 [32], pl. 4, fig. 13. Sitka, Alaska, and other stations; Cuming collection. Reid (2002) corrected and restricted the type locality to Mazatlán, Sinaloa, Mexico. Lectotype, NHMUK 1968217/1 (designated by Reid, 2002: 121, fig. 11a); paralectotypes 1968217/2–4 (n = 3). The Panamic *Nodilittorina aspera* (Philippi, 1846) (Reid, 2002: 121–125, various figs.).
- borealis*, *Lacuna* – Philippi, 1853e: 39–40, pl. 6, fig. 2. Iceland; Bergmann. Synonym of *Lacuna vineta* (Montagu, 1803).
- breviculus*, *Turbo* (*Litorina*) – Philippi, 1844z: 166; 1847b1: 161–162 [19–20], pl. 3, fig. 10, as *Litorina*. Mouth of the Yang-tse River, China; Largilliert. Syntypes, SMF 314686 (n = 2) (9.4 mm x 8.4 mm; 9.5 mm x 8.1 mm). The western Pacific *Littorina* (*Littorina*) *brevicula* (Philippi, 1844) (Reid, 1996: 127–138, figs. 3E, 43–48; Higo et al., 1999: 90; Okutani, 2000: 142–143, fig. 28; Qi, 2004: 32, pl. 14A; Kantor & Sysoev, 2005: 54).
- cecillei*, *Litorina* – Philippi, 1851c: 78. Liew-Kiew Island [Ryukyu Islands, Japan]; Cécille



- via Largilliert. Lectotype, MNHN Paris 5727 (10.9 mm x 7.0 mm) (designated by Reid, 2007a); paralectotype MNHN Paris 23779; possible paralectotypes, Muséum de Rouen 168101033 (n = 6, but no original label). *Echinolittorina* (*Granulilittorina*) *cecillei* (Philippi, 1851) (Reid, 2007a: 66–71, figs. 26G, H, 32–34; Lepage & Buffetaut, 2014).
- cingulata*, *Littorina* – Philippi, 1846g: 142; 1847u: 11–12 [47–48], pl. 6, fig. 5. Australia; Dring; Cuming collection. Lectotype, NHMUK 1968352 (18.6 mm x 12.4 mm) (designated by Rosewater, 1970: 459, pl. 352, fig. 7); two paralectotypes. The Australian *Littoraria* (*Littorinopsis*) *cingulata* (Philippi, 1846) (Reid, 1986: 147–152, figs. 56–59; Wilson, 1993: 145, pl. 18, figs. 7a–c, 8a, b); listed by Higo et al. (1999: 92) as a synonym of *Littoraria* (*Littorinopsis*) *scabra* (Linnaeus, 1758), but still considered by D. G. Reid to be a valid species (personal communication, Nov. 17, 2014).
- conica*, *Littorina* – Philippi, 1846g: 141; 1847u: 9 [45], pl. 6, figs. 1, 2. Java; Cuming collection. Lectotype, NHMUK 1968225/1 (22.2 mm x 14.3 mm) (designated by Rosewater, 1970: 465, pl. 355, figs. 10–11); paralectotypes NHMUK 1968225/2–4 (n = 3). The southeast Asian *Littoraria* (*Palustorina*) *conica* (Philippi, 1846) (Reid, 1986: 182–186, figs. 78–81).
- conspersa*, *Littorina* – Philippi, 1847i: 200–201 [32–33], pl. 4, fig. 14. Realejos, Nicaragua; Petit. Neotype, NHMUK 19990405/1 (12.0 mm x 8.5 mm) (designated by Reid, 2002: 113, fig. 7j). The Panamic *Nodilittorina conspersa* (Philippi, 1847) (Reid, 2002: 113–119, various figures).
- crassior*, *Littorina mauritiana* – Philippi, 1847b1: 165 [23], pl. 3, figs. 15, 17a. No locality stated. Type locality restricted to Australia (Rosewater, 1970: 468). Lectotype, specimen figured by Philippi (fig. 17a), designated by Reid & Williams (2004: 88). Synonym of *Austrolittorina unifasciata* (Gray, 1826) (Wilson, 1993: 146–147, pl. 18, fig. 3, as *Littorina*; Reid & Williams, 2004: 86–92).
- cumingii*, *Trochus* – Philippi, 1846g: 138–139; 1847u: 17 [53], pl. 6, fig. 22, as *Littorina*. Guimaras, Philippine Islands; Cuming. Type species (M) of *Nina* Gray, 1850, *non* Horsfield, 1829 [Lepidoptera]; *Echininus* Clench & Abbott, 1942, replacement name. *Tectarius* (*Echininus*) *cumingii* (Philippi, 1846) (Reid & Geller, 1997: 211).
- debilis*, *Littorina* – Philippi, 1846g: 140; 1847u: 11 [47], pl. 6, fig. 7. Locality unknown; Cuming collection. Lectotype, NHMUK 1968222/1 (9.2 mm x 5.8 mm) (designated by Bandel & Kadolsky, 1982); paralectotypes, NHMUK 1968222/2–4 (n = 3). Synonym of the western Atlantic *Nodilittorina* (*Nodilittorina*) *ziczac* (Gmelin, 1791) (Bequaert, 1943: 15; Bandel & Kadolsky, 1982: 19–21, figs. 5, 6, 14, 15, 18, 19, 45).
- decollata*, *Littorina* – Philippi, 1847i: 196 [28], pl. 4, fig. 3, ex Krauss ms. Natal, South Africa. Credited by Sherborn (1925: 1804) to “Krauss in Philippi”, while the header indicated Krauss as the author, the description was signed by Philippi and the name was indicated as being “in literis,” so Philippi should be regarded as its author. Sherborn also misdated this species as “1846” from Krauss’ book on South African molluscs, but the book did not appear until 1848. Lectotype, Stuttgart Museum ZI 0050277 (formerly MT 107), designated by Janus (1961: 5–6, pl. 3, figs. 3–4); 26 paralectotypes Stuttgart Museum ZI 0050278 (formerly MT 1070–10725); additional type material elsewhere (Herbert & Warén, 1999: 221). Synonym of *Afrolittorina africana* (Philippi, 1847) (Reid & Williams, 2004: 100–102, fig. 15F, lectotype).
- dorbignyana*, *Littorina* – Philippi, 1847b1: 162 [20], pl. 3, fig. 12, as *L. “d’orbignyana”*. Lectotype, NHMUK 1854.10.4.130.1 (23.8 mm x 14.2 mm) (designated by Bandel & Kadolsky, 1982) (probably the specimen figured by d’Orbigny (1842: 210, pl. 15, fig. 7)); paralectotypes, NHMUK 1854.10.4.130.2–5 (n = 4). Synonym of the western Atlantic *Nodilittorina* (*Nodilittorina*) *ziczac* (Gmelin, 1791) (Bequaert, 1943: 15; Bandel & Kadolsky, 1982: 19–21, figs. 5, 6, 14, 15, 18, 19, 45; Rios, 1994: 48, pl. 15, fig. 165a; Reid, 2009: 36).
- elegans*, *Littorina papillosa* – Philippi, 1846x: 140 [10], pl. 2, figs. 5, 7. No locality provided. Syntypes, NHMUK 20130430 (figured specimen, 31.7 mm x 23.6 mm; other syntype, 32.1 mm x 22.3 mm). Synonym of the southwestern Pacific *Tectarius* (*Tectarius*) *coronatus* (Valenciennes, 1832).
- exarata*, *Littorina* – Philippi, 1848f: 63 [57], pl. 7, fig. 8. Locality unknown. Synonym of *Littorina nebulosa* (Lamarck, 1822), from the western Atlantic (Bequaert, 1943: 12).
- fimbriata*, *Risella* – Philippi, 1851b: 32; 1853h: 5–6, pl. 1, figs. 9, 10. Locality unknown. Lectotype, specimen figured by Philippi (pl. 1, fig. 9), designated by Reid (1988: 121). Synonym of *Bembicium vittatum* (Philippi, 1846) (Reid,



- 1988: 121–122, figs. 9–12; Wilson, 1993: 144, pl. 18, fig. 23a, b).
- flammea*, *Litorina* – Philippi, 1847u: 16 [52], pl. 6, fig. 21. China; Largilliert. Lectotype, MNHN Paris 9413 (designated by Reid, 1986: 180); paralectotypes MNHN Paris 9414 (n = 2); SMF 314718 (n = 4) (largest, 13.7 mm x 7.4 mm). Muséum de Rouen 168101055 (n = 6), labeled as types, but no original label. Listed by Higo et al. (1999: 92) as a synonym of *Littoraria* (*Littoraria*) *scabra* (Linnaeus, 1758), but more likely to be a synonym of *Littoraria* (*Palustorina*) *melanostoma* (Gray, 1839), although further study is required of that species (Dong et al., 2015: 318–320).
- flammulata*, *Litorina scabra* – Philippi, 1847o: 222 [38]. Panay & Singapore; Cuming. Listed by Higo et al. (1999: 92) as a synonym of *Littoraria* (*Littorinopsis*) *scabra* (Linnaeus, 1758).
- flavescens*, *Litorina angulifera* – Philippi, 1847o: 224 [40]. Synonym of the amphi-Atlantic *Littoraria angulifera* (Lamarck, 1822) (Bequaert, 1943: 23; Tunnell et al., 2010: 139).
- flavescens*, *Risella* – Philippi, 1851b: 39; 1853h: 7, pl. 1, figs. 17, 18. Norfolk Island; Hanley coll. Lectotype, specimen figured by Philippi (pl. 1, fig. 18), designated by Reid (1988: 125); although Philippi reported this species from the Hanley collection, it was not found by A. Norris in the Hanley collection at the Leeds City Museum. *Bembicium flavescens* Philippi, 1851 (Reid, 1988: 125, figs. 9, 13–15; Wilson, 1993: 143, pl. 18, fig. 22a, b).
- glabrata*, *Litorina* – Philippi, 1846g: 140; 1848f: 62 [56], pl. 7, fig. 5. Païta, Peru; Cuming, & Natal, South Africa; Krauss, Wahlberg. Syn-types, NHMUK 1968220 (n = 4) (Payta, Peru; ex Cuming). Synonym of *Littoraria coccinea* (Gmelin, 1791), from the Indo-Pacific (Reid et al., 2009: 193).
- gracilior*, *Litorina mauritiana* – Philippi, 1847b1: 165 [23], pl. 3, fig. 17b. No locality stated. Lectotype, NHMUK 20020038 (Philippi's figured specimen, 21.7 mm x 12.9 mm), designated by Reid & Williams (2004: 92); paralectotypes NHMUK 20020039 (n = 2). Reid & Williams (2004: 92) concluded that Philippi's species was probably based on specimens of both *Echinolittorina ziczac* (Gmelin, 1791) (western Atlantic) and *Austrolittorina fernandezensis* (Rosewater, 1970) (southeastern Pacific Ocean); to avoid taxonomic disruption, they selected the syn-type "which is undoubtedly a specimen of *E. ziczac*" as the lectotype, and it thus became a synonym of that species.
- granosa*, *Litorina* – Philippi, 1848f: 65 [59], pl. 7, fig. 14. Guinea, Liberia; Busch; Gabon, Largilliert. Lectotype, specimen figured by Philippi (designated by Rosewater, 1981: 44, pl. 2, fig. H). Rosewater (1981: 31) stated in the text, "types in Berlin Museum?" but in the plate caption, he selected Philippi's figured specimen as the lectotype. *Echinolittorina* (*Echinolittorina*) *granosa* (Philippi, 1848) (Reid, 2011: 37–43, figs. 16, 17, 18A, B, 19).
- grisea*, *Risella* – Philippi, 1851b: 31–32; 1853h: 8, pl. 1, figs. 19, 20. Locality unknown. Synonym of *Bembicium nanum* (Lamarck, 1822) (Wilson, 1993: 143, pl. 18, figs. 19a–3).
- gundlachi*, *Litorina* – Philippi, 1849h: 150. Cuba; Gundlach. Synonym of the western Atlantic *Echinolittorina mespillum* (Megerle von Mühlfeld, 1824) (Bequaert, 1943: 21–22, pl. 6, figs. 7–16).
- guttata*, *Litorina* – Philippi, 1847i: 197–198 [29–30], pl. 4, fig. 7, *nom. nov. pro Phasianella punctata* Pfeiffer, 1840, *non Turbo punctatus* Gmelin, 1791, both of which Philippi placed in *Litorina*. Types presumed lost (Reid, 2009). Synonym of *Echinolittorina* (*Fossarilittorina*) *meleagris* (Beck in Potiez & Michaud, 1838) (Reid, 2009: 16–22, figs. 3, 4, 5A, B, 6).
- intermedia*, *Litorina* – Philippi, 1846g: 141; 1847o: 223, pl. 5, figs. 8–11. Red Sea and other stations; Cuming collection. Lectotype, NHMUK 1968343/1, lectotype (Tahiti, ex Cuming) (designated by Reid, 1986: 124, fig. 43); paralectotypes NHMUK 1968343/2–3 (n = 2). The Indo-Pacific *Littoraria* (*Littorinopsis*) *intermedia* (Philippi, 1846) (Reid, 1986: 134–135, figs. 43–47, 2001: 123–125, figs. 12, 13, 17–19, 22; Wilson, 1993: 145, pl. 18, fig. 18; Higo et al., 1999: 92; Okutani, 2000: 138–139, fig. 17; Poppe & Tagaro, 2011b: 590–591, pl. 1286, fig. 6).
- interrupta*, *Litorina ziczac* – Philippi, 1847b1: 164 [22], "ex Adams ms". This name was listed as "C. B. Adams in Philippi" by Bandel & Kadolsky (1982) and by Reid (2009), but the text is clearly by Philippi, who did not even make clear which Adams was being mentioned (both C. B. Adams and Henry Adams are known to have provided material from Jamaica). While Clench & Turner (1950: 294) recognized the species as described by Philippi and not by C. B. Adams, they did not cite Philippi's original description, but instead



- referred to the page in the later monograph by Küster on *Litorina* (1856: 24, pl. 3, figs. 14, 14, in Küster & Weinkauff, 1853–1882) as if it were by Philippi, and incorrectly designated one of the specimens figured therein as “lectotype”. In the absence of other type material, Reid (2009) designated a neotype (MCZ 186123) (9.2 mm x 6.0 mm). The name was considered to have been published in synonymy and made available under ICZN Code Article 11.6 (1999). *Nodilittorina* (*Nodilittorina*) *interrupta* (Philippi, 1847) (Bandel & Kadolsky, 1982: 23–25, figs. 5, 7, 16, 17, 23–26; Reid, 2009: 50–56, figs. 2D, 16C, D, 22–24), both as “C. B. Adams in Philippi, 1847”.
- knysnaensis*, *Litorina* – Philippi, 1847i: 196 [28], pl. 4, fig. 4, ex Krauss ms. Natal, South Africa. Credited by Sherborn (1927: 3320) to “Krauss in Philippi”, while the header indicated Krauss as the author, the description was signed by Philippi and the name was indicated as being “in litt.”, so Philippi should be regarded as its author. Sherborn also misdated this species as 1846 from Krauss’ book on South African molluscs, but the book did not appear until 1848. Lectotype, Stuttgart Museum MT 108, designated by Janus (1961: 6, pl. 3, figs. 5–6); 29 paralectotypes Stuttgart Museum MT 1080–10829; additional type material elsewhere (Herbert & Warén, 1999: 224). Synonym of *Nodilittorina* (*Echinolittorina*) *africana* (Philippi, 1847) (Janus, 1961: 6), now *Afrolittorina africana* (Philippi, 1847).
- laevis*, *Litorina* – Philippi, 1846g: 140; 1847u: 10–11 [46–47], pl. 6, fig. 6. Locality unknown; Cuming collection. Syntypes, NHMUK 1968221 (locality?, ex Cuming) (18.4 mm x 12.2 mm; 14.5 mm x 10.7 mm).
- lemniscata*, *Litorina* – Philippi, 1846g: 139; 1847u: 14–15 [50–51], pl. 6, fig. 16. “Cuba?”; Cuming collection. Lectotype, NHMUK 1968216/1 (8.3 mm x 5.7 mm); paralectotypes, NHMUK 1968216/2–3 (n = 2). *Echinolittorina lemniscata* (Philippi, 1846), which actually came from the Islas Galápagos, Ecuador, and has thus far been treated as a senior synonym of *E. galapagensis* (Stearns, 1891) (Reid, 2011: 44).
- leucostricta*, *Litorina* – Philippi, 1847b1: 162 [20], pl. 3, fig. 11. Locality unknown; Bombay India (Rosewater, 1970). Lectotype, Philippi’s figure (Rosewater, 1970); Staatliche Naturhistorische Sammlung Dresden 1591, paralectotype. *Echinolittorina* (*Granulilittorina*) *leucostricta* (Philippi, 1847) (Reid, 2007a: 78–84, figs. 40, 41, 42A, B, 43).
- lineata*, *Litorina angulifera* – Philippi, 1847o: 224 [40], pl. 5, fig. 15. Syntypes, NHMUK 198322 (n = 2) (“Loanda, on mangrove trees” = Luanda, Angola). Synonym of the amphiatlantic *Littoraria angulifera* (Lamarck, 1822) (Bequaert, 1943: 23).
- lividum*, *Bembicium* – Philippi, 1846s: 131; 1853h: 10, pl. 1, figs. 27, 28, as *Risella livida*. Australia. Synonym of *Bembicium melanostoma* (Gmelin, 1791) (Wilson, 1993: 143, pl. 18, fig. 24a).
- lutea*, *Litorina scabra* – Philippi, 1847o: 222 [38], pl. 5, fig. 6. Masbate, Philippine Islands & Canton. *Littoraria* (*Littorinopsis*) *lutea* (Philippi, 1847) (Reid, 2001: 119).
- malaccana*, *Litorina* – Philippi, 1847u: 15 [51], pl. 6, fig. 17. Pulo Pinang; Th. Philippi. Lectotype, NHMUK 20050028/1 (10.9 mm x 7.3 mm) (designated by Reid, 2007a); paralectotypes, NHMUK 20050028/2 (n = 6). *Echinolittorina* (*Granulilittorina*) *malaccana* (Philippi, 1847) (Reid, 2007a: 55–62, figs. 26C, D, 27–29).
- marmorata*, *Litorina picta* – Philippi, 1846g: 167, non *L. marmorata* Pfeiffer, 1839. Hawaiian Islands & Luzon, Philippine Islands (type locality restricted to the latter: Rosewater, 1970). “Lectotype”, the specimen in Philippi, 1847b1, pl. 3, fig. 26 (Rosewater, 1970), but that would also be the only figure for *Litorina picta*.
- millegrana*, *Litorina* – Philippi, 1848f: 65–66 [59–60], pl. 7, fig. 15. Red Sea; Hemprich & Ehrenberg. ZMB 112.713, lectotype (designated by Rosewater, 1970, based on Philippi’s figure of this specimen). *Echinolittorina millegrana* (Philippi, 1848) (Wilson, 1993: 147, pl. 18, fig. 9a, b, as *Nodilittorina*; Reid, 2007a: 139–143, figs. 66G, H, 71–73).
- modesta*, *Litorina* – Philippi, 1846g: 141; 1847u: 12–13 [48], pl. 6, fig. 12. Sitka, Alaska; Barclay & Mauritius; Cuming collection. Both of Philippi’s localities were in error, and the type locality was restricted to Mazatlán, Sinaloa, Mexico, by Reid (2002). Lectotype, NHMUK 1968224/1 (“Sitka”) (19.6 mm x 13.6 mm) (designated by Reid, 2002: 111, fig. 7e); paralectotypes, NHMUK 1968224/2–4 (“Sitka”) (n = 3); “possible paralectotypes” NHMUK 19990404 (“Sitka”) (n = 3). The Panamic *Echinolittorina modesta* (Philippi, 1846) (Reid, 2002: 111–113, various figs.).
- natalensis*, *Litorina* – Philippi, 1847b1: 160 [18], pl. 3, fig. 4, ex Krauss ms. Natal, South Africa.



- Credited by Sherborn (1928: 4261) and by Reid (2007a: 31) to "Krauss in Philippi", while the header indicated Krauss as the author, the description was signed by Philippi and the name was indicated as being "in litt.", so Philippi should be regarded as its author. Lectotype, Stuttgart Museum ZI0050942 (formerly MT 109), designated by Janus (1961: 7, pl. 3, figs. 7–8); 12 paralectotypes Stuttgart Museum ZI0050943 (formerly MT 1090–10912); MCZ 154107 (n = 33); additional type material elsewhere (Herbert & Warén, 1999: 221; Reid, 2007a: 31). *Echinolittorina* (*Granulilittorina*) *natalensis* (Philippi, 1847) (Reid, 2007a: 31–37, figs. 13, 14, 15A–D, 16).
- ovulum*, *Rissoa* – Philippi, 1844z4: 51, [87], pl. 3, fig. 12. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. *Tricolia ovulum* (Philippi, 1844) (Anderson, 1959: 70–71); *Cirsope* (*Cirsope*?) *ovulum* (Philippi, 1844) (Janssen, 1978a: 35–36, 1978b: 151–152, pl. 10, fig. 22).
- pallescens*, *Littorina* – Philippi, 1846g: 142; 1847u: 10 [46], pl. 6, fig. 4. Mindanao, Philippine Islands; Cuming. Lectotype, NHMUK 1968277/1 (designated by Rosewater, 1970: 459, pl. 352, fig. 12); paralectotypes NHMUK 1968277/2–3 (n = 2). Note: Philippi, 1847u: 10 [46] originally listed *Littorina filosa* G. B. Sowerby I, 1832, for the description of pl. 6, fig. 4; a "corrected" sheet replaced that with *L. pallescens* Philippi, 1846. The Indo-Pacific *Littoraria* (*Littorinopsis*) *pallescens* (Philippi, 1846) (Reid, 1986: 108–118, figs. 34–38, 2001: 119–120; Higo et al., 1999: 92; Okutani, 2000: 138–139, fig. 16; Swennen et al., 2001: 113, fig. 307; Wilson, 1993: 145, pl. 18, fig. 4a–d; Poppe & Tagaro, 2011b: 590–591, pl. 1286, figs. 4, 5).
- parvula*, *Littorina* – Philippi, 1849h: 149. Panama; E. B. Philippi. *Nomen dubium*; possible senior synonym of *Nodilittornia apicina* (Menke, 1851), but types lost (Reid, 2002: 135, 137).
- paytensis*, *Littorina* – Philippi, 1847b1: 166 [24], pl. 3, fig. 25. Païta, Peru; Petit. *Nodilittorina paytensis* (Philippi, 1847) (Reid, 2002: 140–142, several figs.). Lectotype: Philippi's fig. 25, central shell (designated by Reid, 2002).
- picta*, *Littorina* – Philippi, 1846g: 139; 1847b1: 166–167 [24–25], pl. 3, fig. 26, *non L. obtusata picta* Menke, 1845. Hawaii; Cuming collection. Lectotype, NHMUK 1968324/1 (designated by Rosewater, 1970: 504, pl. 386, figs. 7–8; erroneously indicated as a "neotype" by Reid, 2007a: 129, fig. 67a) (9.7 mm x 6.8 mm); paralectotypes, NHMUK 1968324/2–3 (n = 2). The Hawaiian *Nodilittorina* (*Granulilittorina*) *hawaiiensis* Rosewater & Kadolsky, 1981, a replacement name (Reid, 2007a: 129–133, figs. 23, 66C, D, 67, 68; Severns, 2011: 102–103, fig. 2).
- pictum*, *Bembicium* – Philippi, 1846s: 132; 1853h: 6, pl. 1, figs. 11, 12, as *Risella picta*. For *Trochus nanus* Lamarck *sensu* Quoy & Gaimard, 1832, *non* Lamarck, 1822; thus, it is a new species, not a new name. Tasmania. Synonym of *Bembicium nanum* (Lamarck, 1822) (Wilson, 1993: 143, pl. 18, figs. 19a–3).
- planaxis*, *Littorina* – Philippi, 1847i: 201 [33], pl. 4, fig. 16, ex Nuttall ms, *non* G. B. Sowerby I, 1844. California. Lectotype, NHMUK 1912.4.12.30.1 (designated by Rosewater, 1978: 123, pl. 1, fig. 2, as "holotype") (17.4 mm x 13.6 mm); paralectotypes, NHMUK 1912.4.12.30.2–4. *Littorina keenae* Rosewater, 1978, *nom. nov.*, which is the type species (OD) of *Planilittorina* Reid, 1989. This species was discussed by Reid (1996: 53–60, figs. 3B, 13–16; 2007b: 764).
- plicatula*, *Risella* – Philippi, 1851b: 39–40; 1853h: 9, pl. 1, figs. 23, 24. Norfolk Island; Hanley coll. Lectotype, specimen figured by Philippi (pl. 1, fig. 23), designated by Reid (1988: 125). Although Philippi reported this species from the Hanley collection, it was not found by A. Norris in the Hanley collection at the Leeds City Museum. Synonym of *Bembicium flavescens* Philippi, 1851 (Reid, 1988: 125, figs. 9, 13–15; Wilson, 1993: 143, pl. 18, fig. 22a, b).
- porcata*, *Littorina* – Philippi, 1846g: 139; 1847u: 14 [50], pl. 6, fig. 15. Galapagos Islands; Cuming. Lectotype, NHMUK 1968218/1 (designated by Reid, 2002: 97, fig. 1j); 1 paralectotype, NHMUK 1968218/2; probable paralectotypes, NHMUK 1998193 (no locality; ex Cuming) (n = 2). The Galapagos *Echinolittorina porcata* (Philippi, 1846) (Reid, 2002: 97–101, various figs.).
- punctata*, *Littorina angulifera* – Philippi, 1847o: 224 [40], pl. 5, fig. 13, *non* Philippi, 1846. Syntypes, NHMUK 198325 (Senegal; Cuming) (largest, 32.4 mm x 20.8 mm). Synonym of the amphi-Atlantic *Littoraria angulifera* (Lamarck, 1822) (Bequaert, 1943: 23).
- punctata*, *Littorina intermedia* – Philippi, 1846g: 141; 1847o: 223 [39], pl. 5, fig. 11. Red Sea?; Cuming collection (additional localities listed in 1847: Tahiti; Elizabeth Island; Natal). Synonym of the Indo-Pacific *Littoraria* (*Littorinop-*



- sis intermedia* (Philippi, 1846) (Reid, 1986: 134–135; Higo et al., 1999: 92).
- punctata*, *Litorina scabra* – Philippi, 1847o: 222 [38], pl. 5, fig. 5, *non* Philippi, 1846. Punkten, Masbate, Singapore. Listed by Higo et al. (1999: 92) as a synonym of *Littoraria* (*Littorinopsis*) *scabra* (Linnaeus, 1758).
- puncticulata*, *Litorina* – Philippi, 1847i: 201 [33], pl. 4, fig. 15. Realejos, Nicaragua; Petit. Synonym of the Panamic *Nodilittorina conspersa* (Philippi, 1847); types not found (Reid, 2002: 113).
- pusilla*, *Litorina* – Philippi, 1847b1: 164 [22], pl. 3, fig. 23, *non* M'Coy, 1844. Brazil or Hawaii; Largilliert. Synonym of *Nodilittorina* (*Nodilittorina*) *lineolata* (d'Orbigny, 1840) (Bandel & Kadolsky, 1982: 21–23, figs. 1A, 3A, 5, 7, 20–22; Reid, 2009: 28–33, figs. 10–13). Type locality restricted to Brazil by Bandel & Kadolsky, 1982).
- quadriseiata*, *Litorina papillosa* – Philippi, 1846x: 140 [10], pl. 2, fig. 2. Zanzibar. Syntypes, NHMUK 20130429 (n = 3) (largest, 39.8 mm x 29.8 mm). Type locality in error; synonym of the southwestern Pacific *Tectarius* (*Tectarius*) *coronatus* (Valenciennes, 1832).
- rubra*, *Litorina angulifera* – Philippi, 1847o: 224 [40], pl. 5, fig. 12. Syntypes, NHMUK 198324/1–3 (Honduras, ex Cuming) (figured syntype, 26.3 mm x 17.5 mm). Synonym of the amphi-Atlantic *Littoraria angulifera* (Lamarck, 1822) (Bequaert, 1943: 23). This species and the next are junior homonyms (ICZN Article 57.2 (1999)), but as each is already a junior synonym of another species, no re-naming is required.
- rubra*, *Litorina scabra* – Philippi, 1847o: 222 [38], pl. 5, fig. 12. Mindoro, Philippine Islands, & Canton. Listed by Higo et al. (1999: 92) as a synonym of *Littoraria* (*Littorinopsis*) *scabra* (Linnaeus, 1758).
- rustica*, *Litorina papillosa* – Philippi, 1846x: 140 [10], pl. 2, fig. 3. Point Swan, North coast of Australia. Lectotype, NHMUK 20130428/1 (designated by Rosewater, 1972: 523); paralectotypes, NHMUK 20130428/2–3. The northwestern Australian *Tectarius rusticus* (Philippi, 1846) (Abbott & Dance, 1982: 58; Wilson, 1993: 148, pl. 18, fig. 20).
- sayi*, *Litorina* – Philippi, 1846g: 140; 1847u: 12 [48], pl. 6, fig. 11. Florida; Say; Cuming collection. Syntypes, NHMUK 1968223 (n = 4). Synonym of the western Atlantic *Littoraria irrorata* (Say, 1822).
- sieboldii*, *Litorina* – Philippi, 1846g: 142; 1847u: 9–10 [45–46], pl. 6, fig. 3. Japan; Siebold; Cuming collection. NHMUK 1968278, holotype (Reid, 1986: 108, fig. 34a) (28.9 mm x 17.6). Synonym of the Indo-Pacific *Littoraria* (*Littorinopsis*) *pallidescens* (Philippi, 1846) (Reid, 1986: 108–118; Higo et al., 1999: 92).
- sinensis*, *Litorina* – Philippi, 1847u: 16–17 [52–55], pl. 6, fig. 23. China; Largilliert. Lectotype, MNHN Paris 5782 (designated by Reid, 1986: 200, fig. 90d) (13.2 mm x 9.1 mm); paralectotypes MNHN Paris 5783 (n = 2); Muséum de Rouen 168101030 (n = 22). *Littoraria* (*Palustorina*) *sinensis* (Philippi, 1847) (Reid, 2001: 129–134, figs. 38–52, 56–64, 68).
- sitkana*, *Litorina* – Philippi, 1846g: 140; 1847u: 13 [49], pl. 6, figs. 13, 18, as *L. sitchana*. Sitka, Alaska; Barclay; Cuming collection. NHMUK 1968219/1, lectotype (designated by Reid, 1996: 146, fig. 56A) (12.3 mm x 11.9 mm); NHMUK 1968219/2, paralectotype. Type species (OD) of *Littorivaga* Dall, 1918, a synonym of *Neritrema* Récluz, 1869. The North Pacific *Littorina* (*Neritrema*) *sitkana* Philippi, 1846 (Reid, 1996: 146–162, frontispiece, figs. 5, 54–58; Higo et al., 1999: 90; Okutani, 2000: 142–143, fig. 31; Kantor & Sysoev, 2005: 55; Reid, 2007b: 765–766).
- spinulosa*, *Litorina* – Philippi, 1847u: 17 [53], pl. 6, fig. 24. Manila; Gruner. *Echinus cumingii spinulosus* (Philippi, 1847) (Higo et al., 1999: 93; Okutani, 2000: 138–139, fig. 12, as “1846”) or *Tectarius* (*Echinus*) *spinulosus* (Philippi, 1847) (Reid & Geller, 1997: 233).
- strigata*, *Litorina angulifera* – Philippi, 1847o: 224 [40], pl. 5, fig. 14. Syntypes, NHMUK 198323/1–4 (n = 4) (River Gambia, ex Cuming) (figured syntype, 36.6 mm x 23.4 mm). Synonym of the amphi-Atlantic *Littoraria angulifera* (Lamarck, 1822) (Bequaert, 1943: 23).
- strigata*, *Litorina intermedia* – Philippi, 1846g: 141; 1847o: 223 [39], pl. 5, figs. 8–10. Jimamailan, Negros Island, Philippine Islands; Cuming collection. Lectotype, NHMUK 1968353 (designated by Reid, 1986: 209, fig. 95) (14.0 mm x 8.6 mm) (Rosewater, 1970: 456, pl. 352, fig. 8, erroneously designated this lot as the lectotype of *L. intermedia*). *Littoraria* (*Palustorina*) *strigata* (Philippi, 1846) (Reid, 1986: 209–216, figs. 95–98; 2001: 135; Swennen et al., 2001: 113, fig. 309).
- subinermis*, *Litorina papillosa* – Philippi, 1846x: 141 [11]. No locality provided. *Tectarius bul-latus* “Martyn” (Tryon, 1887a: 257), which is now *T. grandinatus* (Gmelin, 1791), Indo-Pacific (Rosewater, 1972: 523).



*subnodosa*, *Litorina* – Philippi, 1847b1: 161 [19], pl. 3, figs. 8, 9. Red Sea. Lectotype, specimen in Philippi's fig. 9 (designated by Rosewater, 1970: 495–496); paralectotypes, ZMB 2395 (n = 3). *Echinolittorina* (*Granulilittorina*) *subnodosa* (Philippi, 1847) (Reid, 2007a: 31–44, figs. 15E, F, 16, 19, 20).

*sulcosa*, *Litorina* – Philippi, 1887a: 81 [1887b: 76], pl. 8, fig. 20. Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.849 (labeled as “lectotipo”); SGO.PI.4662–4675 (each labeled as “paralectotipo”).

*sulculosa*, *Litorina* – Philippi, 1846g: 142; 1847u: 18 [54], pl. 6, fig. 10. Australia; Dring; Cuming collection. Lectotype, NHMUK 1968279/1 (designated by Rosewater, 1970: 459, pl. 352, figs. 17–18) (17.1 mm x 10.3 mm); paralectotypes NHMUK 1968279/2–4; NHMUK 1968280/1–2. The Australian *Littoraria* (*Palustorina*) *sulculosa* (Philippi, 1846) (Reid, 1986: 194–200, figs. 86–89; Wilson, 1993: 146); listed by Higo et al. (1999: 92) as a synonym of *Littoraria* (*Littorinopsis*) *scabra* (Linnaeus, 1758), but considered by D. G. Reid to be a valid species.

*suturalis*, *Litorina scabra* – Philippi, 1847o: 222 [38], pl. 5, fig. 7. Kängaruh Island, Canton, etc. Listed by Higo et al. (1999: 92) as a synonym of *Littoraria* (*Littorinopsis*) *scabra* (Linnaeus, 1758).

*syriaca*, *Litorina* – Philippi, 1847b1: 165 [23], pl. 3, figs. 21, 22. Syria; F. Krauss. Syntypes, Staatliches Museum für Naturkunde Stuttgart ZI0050270 (n = 6). Synonym of *Echinolittorina* (*Amerolittorina*) *punctata* (Gmelin, 1791) (Priolo, 1953b: 179 [124]; Sabelli et al., 1990: 146; Reid, 2011: 16–24, figs. 4E–H, 6–8).

*tenuis*, *Litorina* – Philippi, 1846g: 141–142; 1847u: 18 [54], pl. 6, fig. 8. Ticao, Philippine Islands; Cuming. Syntypes, NHMUK 1968276 (n = 2) (14.4 mm x 9.1 mm; 13.0 mm x 7.9 mm). Synonym of *Littoraria* (*Littoraria*) *undulata* (Gray, 1839) (Higo et al., 1999: 91).

*tessellata*, *Litorina* – Philippi, 1847o: 226–227 [42–43], pl. 5, fig. 26, *nom. nov. pro Littorina undulata* d'Orbigny, 1842, *non* Gray, 1839. The western Atlantic *Littoraria tessellata* (Philippi, 1847) (Bequaert, 1943: 13: pl. 4, figs. 8–10, as a subspecies of *L. undulata*; Bandel & Kadolsky, 1982: 38, figs. 40, 41, as a full species).

*thorpeana*, *Lacuna* – Philippi, 1853e: 48, pl. 6, fig. 14. England. Philippi established this taxon for specimens he received that were misidentified as “*Lacuna patula*” Thorpe, 1844 (which is now regarded as a *nomen*

*dubium*; Coan & Kabat, 2012: 328). Synonym of *L. pallidula* (da Costa, 1778) (Tryon, 1887a: 265).

*ventricosa*, *Litorina* – Philippi, 1847u: 15–16 [51–52], pl. 6, fig. 19, *non Litorina scabra* var. *ventricosa* Philippi, 1847o. Pulo Pinang; Th. Philippi. Lectotype, Philippi's figure (designated by Rosewater, 1970); Staatliches Museum für Naturkunde Stuttgart ZI0050272, 2 paralectotypes. Synonym of *Echinolittorina* (*Granulilittorina*) *vidua* (Gould, 1859) (Reid, 2007a: 111–119, figs. 55E, F, 59–61).

*ventricosa*, *Litorina scabra* – Philippi, 1847o: 222 [38], pl. 5, fig. 8. China, Mindanao, Tonga Tabu, New Ireland, New Guinea, “aber auch im Altguinea und am Senegal” [Atlantic coast of Africa]. Listed by Higo et al. (1999: 92) as a synonym of *Littoraria* (*Littorinopsis*) *scabra* (Linnaeus, 1758).

*vera*, *Litorina papillosa* – Philippi, 1846x: 141. No locality provided. *Tectarius bullatus* “Martyn” (Tryon, 1887a: 257), which is now *T. grandinatus* (Gmelin, 1791), Indo-Pacific (Rosewater, 1972: 523).

*vilis*, *Litorina* – Philippi, 1846x: 145 [15], pl. 1, fig. 21, ex Menke ms. Locality unknown. Synonym of *Nodilittorina pyramidalis* (Quoy & Gaimard, 1833) (Wilson, 1993: 147, pl. 18, fig. 5a, b).

*vittata*, *Litorina* – Philippi, 1848f: 64 [58], pl. 7, fig. 11. “*Litus Britanniae gallicae*”. Synonym of *Littorina* (*Neritrema*) *fabalis* (W. Turton, 1825); type material not traced (Reid, 1996: 227–245, figs. 3H, 82–88; Kantor & Sysoev, 2005: 54).

*vittatum*, *Bembicium* – Philippi, 1846s: 131; 1853h: 9, pl. 1, figs. 25, 27, as *Risella vittata*. Adelaide, Australia; Gruner. Lectotype, specimen figured by Philippi (pl. 1, fig. 25), designated by Reid (1988: 121). *Bembicium vittatum* (Philippi, 1846) (Reid, 1988: 121–122, figs. 9–12; Wilson, 1993: 144, pl. 18, figs. 23a, b).

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“*Fectaria*” – Philippi, 1846x: 139 [9]. Spelling error for *Tectaria* Guérin-Ménéville, 1835, which in turn was an incorrect spelling of *Tectarius* Valenciennes, 1833.

“*Melaraphis*” – Philippi, 1836a: 189, ex Stentz ms. In synonymy; error pro *Melarhappe* Menke, 1828.

“*zebra*, *Littorina*” – Dall (1909: 285) listed this as a Philippi species, and treated it as a junior synonym of *L. peruviana* Lamarck, 1822. However, this was Dall's error for *L. zebra* Donovan, 1825.



"ziczac, *Litorina*" – Philippi, 1847b1: 162–163.

This was listed by Sherborn (1932: 7043) as if it were a name independent from its availability from Gmelin (1791), but it would have been at most a misuse.

#### Annulariidae

*thoreyanum*, *Cyclostoma* – Philippi, 1851b: 31.

Bolivia; Thorey. Solem (1960: 421) thought that the type locality was "probably ... erroneous" and "of questionable validity." Watters (2006: 72, 508) listed it as questionably from Bolivia, and referred it to his new genus, *Gouldipoma*.

#### Skeneopsidae

*gouldii*, *Skenea* – Philippi, 1853f: 10, unfigured.

New species based on *Skenea serpuloides* (Montagu, 1808), *sensu* Gould (1841: 247, fig. 189), *non* Montagu, 1808. Massachusetts. Synonym of the North Atlantic *Skeneopsis planorbis* (Fabricius, 1780).

#### Naticidae

*Uber* – Philippi, 1853a: 497, *ex* Humphreys ms. Type species (OD): *Nerita mammilla* Linnaeus, 1758, as "*Natica*". Objective junior synonym of *Polinices* Montfort, 1810, which has the same type species.

*acuta*, *Natica* – Philippi, 1845i: 65; 1845s: 41–42 [7–8], pl. 2, fig. 3, *non* Deshayes, 1838. Strait of Magellan, Chile. Renamed as *Natica philippiana* Nyst, 1845. Type material not found in MNHNS (Pastorino, 2005b: 233). Synonym of *Tectonatica impervia* (Philippi, 1845) (Pastorino, 2005b: 231–234).

*adansonii*, *Natica* – Philippi, 1849i: 155; 1851f: pl. 15, fig. 6; 1852c: 104–105. Gabon in Guinea; Largilliert.

*alba*, *Natica* – Philippi, 1842d: 16–17 [4–5], pl. 1, fig. 13, *ex* Loven ms, *non* Gray, 1826, *non* Potiez & Michaud, 1838. Greenland. Probably a junior synonym of the circumboreal *Euspira pallida* (Broderip & Sowerby, 1829) (A. R. Kabat, pers. obs.).

*amiculata*, *Natica* – Philippi, 1849i: 155; 1851f: pl. 14, fig. 4; 1852c: 98. Païta, Peru; E. B. Philippi. Marincovich (1977: 258–259) concluded that this species was a senior synonym of *Natica ravida* Souleyet, 1852, which has the same type locality, but he then erroneously stated "BM(NH), three syntypes, illustrated by Keen (1971)." In fact, Keen (1971: 480, fig. 881) illustrated a syntype of

*N. ravida*, and made no mention of Philippi's type material; instead, Keen (1971: 478) treated *N. amiculata* as a junior synonym of *Polinices panamensis* (Récluz, 1844).

*ampla*, *Natica* – Philippi, 1849i: 156; 1850r: pl. 6, fig. 2; 1852c: 41–42. Locality unknown. The Indo-Pacific *Glossaulax didyma ampla* (Philippi, 1849) (Higo et al., 1999: 144).

*antoni*, *Natica* – Philippi, 1851b: 48; 1853c: 144, pl. 19, fig. 18. Liew-Kiew Island, China [Ryukyu Islands, Japan]; Largilliert. Synonym of *Natica gualtieriana* (Récluz, 1844) (Kilburn, 1976: 835–837; Higo et al., 1999: 147, as "*N. antonii*"; Kabat, 2000: 354), or a valid species (Severns, 2011: 110–111, fig. 3).

*articulata*, *Natica* – Philippi, 1852c: 119–120; 1851f: pl. 17, figs. 4, 8. Zanzibar & Seychelles [Seychelles]. The uncaptioned plate appeared one year before the text (1852) making the name available. Either a synonym of the western Pacific *Naticarius alapapilionis* (Röding, 1798) (Wilson, 1993: 217, pl. 36, fig. 1) or a valid species, *Naticarius articulatus* (Philippi, 1852) (Higo et al., 1999: 147), which occurs from the Indian Ocean to Japan.

*atacamensis*, *Natica* – Philippi, 1860a: 186–187 [1860b: 168], Zool. pl. 7, fig. 20. Mejillones, Chile; Recent.

*atrocyanea*, *Natica* – Philippi, 1845i: 64; 1845s: 41 [7], pl. 2, fig. 1; 1850r: pl. 8, fig. 7; 1852c: 53. Strait of Magellan, Chile. Holotype, MNHNS 189 (broken, 37.7 mm x 32.0 mm) (Pastorino, 2005b: figs. 18–19). Synonym of *Natica limbata* d'Orbigny, 1839 (Castellanos & Landoni, 1990: 23–24; Rios, 1994: 80, pl. 26, fig. 309; Forcelli, 2000: 78; Pastorino, 2005b: 229–231, "genus uncertain").

*avellana*, *Natica* – Philippi, 1852c: 75–76; 1850r: pl. 11, fig. 14. Locality unknown. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available.

*balteata*, *Natica melanostoma* – Philippi, 1852c: 31, 34–35; 1849z4: pl. 4, figs. 15, 16. No locality stated. The uncaptioned plate (1849) appeared three years before the text (1852) making the name available.

*barrosi*, *Natica* – Philippi, 1887a: 88 [1887b: 83], pl. 10, fig. 9. Río Rapel, Chile; Diego Barros Arana; Tertiary. Syntypes, SGO.PI.26 (n = 3, from Matanzas, which includes the Río Rapel).

*bicolor*, *Natica* – Philippi, 1849i: 156–157; 1850r: pl. 6, fig. 4; 1852c: 43. China. Possible syntype, NHMUK 1923.7.13.16 ("Florida" *ex* Reissner) (25.8 mm x 29.4 mm); this specimen could be mislocalized and a mis-



- identified specimen of the western Atlantic *Neverita duplicata* (Say, 1822). Either a junior synonym of the Indo-Pacific *Polinices* (*Glossaulax*) *didyma* (Röding, 1798) (Kilburn, 1976: 860), or a valid species, *Glossaulax bicolor* (Philippi, 1849) (Higo et al., 1999: 145; Okutani, 2000: 254–255, fig. 24, as “1848”).
- brocchiana*, *Natica* – Philippi, 1852c: 50–51; 1850r: pl. 8, fig. 2. Mediterranean. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. Synonym of *Euspira fusca* (Blainville, 1825) (Priolo, 1963: 33–35 [469–471]; Sabelli et al., 1990: 170; Bouchet & Warén, 1993: 776; Kantor & Sysoev, 2005: 59).
- caprae*, *Natica* – Philippi, 1852c: 56; 1850r: pl. 9, fig. 2. Mazatlán, Sinaloa, Mexico. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. Syntypes, MHNHS 61.567 (n = 2) (fide Marincovich, 1977: 300; not seen in March 2014). *Mammilla caprae* (Philippi, 1852) (Marincovich, 1977: 299–300, pl. 25, figs. 13–14).
- caribaea*, *Natica* – Philippi, 1853b: 234; 1853c: 127–128, pl. 18, fig. 8. St. John’s [Virgin Islands], Caribbean; Cuming coll. Misspelled as *N. caribbaea* by Reeve (1855: pl. 25, fig. 118). Synonym of *Polinices lacteus* (Guilding, 1834) (A. R. Kabat, pers. obs.).
- casta*, *Natica* – Philippi, 1852c: 117–118; 1851f: pl. 17, fig. 1. Locality unknown. The uncaptioned plate (1851) appeared one year before the text (1852) making the name available. Probably an Indo-Pacific *Polinices* (A. R. Kabat, pers. obs.).
- catenata*, *Natica* – Philippi, 1853b: 233; 1853c: 130, pl. 18, fig. 11. Locality unknown; Cuming coll. Possibly Mazatlán, Sinaloa, Mexico (Ponton, 1868). Synonym of the Panamic *Naticarius grayi* (Philippi, 1852) (Keen, 1971: 274–275, fig. 863, as *Natica*; Marincovich, 1977: 385–389, pl. 37, fig. 12, pl. 40, fig. 1).
- chiloensis*, *Natica* – Philippi, 1887a: 89 [1887b: 84], pl. 10, fig. 12. Cueva de Cucao, Chiloé, Chile; Tertiary. Syntypes, SGO.PI.4591, 4592 (n = 1, each labeled as “paralectotipo”). Griffin & Pastorino (2013: 513) determined that subsequent records of this species from Punta Arenas, Patagonia, Chile, were misidentifications for *Polinices puntarenas* Ihering, 1907. *Neverita chiloensis* (Philippi, 1887), Miocene (Frassinetti, 2001: 80, figs. 8–11; 2004: 76).
- citrina*, *Natica* – Philippi, 1851b: 49; 1853c: 143–144, pl. 19, fig. 17. Locality unknown.
- The Japanese *Polinices citrinus* (Philippi, 1851) (Higo et al., 1999: 144, as “1853”).
- cuadrae*, *Natica* – Philippi, 1887a: 85 [1887b: 80], pl. 9, fig. 24 [labeled as “*N. lepida*” on pl.]. Hualpen and Tumbez, Chile; Cretaceous. Syntypes, SGO.PI.68 (n = 1, from Tumbez, labeled as “holotipo”); SGO.PI.45 (n = 1, from Hualpen). Possibly a junior synonym of *Gyrodos chilina* (d’Orbigny, 1847) (Wilckens, 1904: 200).
- cygnea*, *Natica* – Philippi, 1852c: 80–81; 1850r: pl. 12, fig. 6. Locality not stated. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. Synonym of the western Pacific *Polinices mammilla* (Linnaeus, 1758) (Kabat, 1990: 16–19, fig. 3A, B; Wilson, 1993: 220, pl. 36, fig. 30; Higo et al., 1999: 144).
- darwini*, *Natica* – Philippi, 1887a: 85–86 [1887b: 80], pl. 9, fig. 28, *non* Hutton, 1886. Tumbez and Hualpen, Chile; Francisco J. Ovalle; Cretaceous. Syntypes, SGO.PI.73 (n = 2, from Hualpen). Renamed *Natica tumbeziana* Ihering (1907: 152–153). Ihering, earlier in the same paper (1907: 89), stated “*Polynices carolodarwini* lh. par *P. darwini* Hutton”, but there appears to have been no need to rename Hutton’s species (Parodiz, 1996: 275). Synonym of *Gyrodos chilina* (d’Orbigny, 1846) (Wilckens, 1904: 200).
- decora*, *Natica* – Philippi, 1852c: 118; 1851f: pl. 17, fig. 2. Locality unknown. The uncaptioned plate (1851) appeared one year before the text making the name available. Synonym of the Indo-Pacific *Tanea euzona* (Récluz, 1844) (Kilburn, 1976: 854–855; Higo et al., 1999: 148).
- depressus*, *Sigaretus* – Philippi, 1844q: 144 [2], pl. 1, fig. 3. Locality not stated.
- dilatata*, *Natica* – Philippi, 1841f: 20; 1844z4: 20, [87], pl. 3, fig. 20. Tertiary near Wilhelms-höhe, Hessen, Germany [Late Oligocene]. *Lunatia dilatata* (Philippi, 1841) (Janssen, 1979a: 193–194, pl. 14, figs. 82, 83; Rust, 1999: 23, pl. 2, fig. 1, both dated the species from 1843; Anderson, 1960b: 83–84, as *Polinices* (*Euspira*) *dilatata*). Type material lost (R. Janssen, pers. comm., April 2013).
- diminutiva*, *Natica* – Philippi, 1887a: 90–91 [1887b: 85], pl. 9, fig. 22. Navidad, Chile; Tertiary [Miocene].
- distorta*, *Natica* – Philippi, 1887a: 86–87 [1887b: 81], pl. 9, fig. 27. Locality unknown, Chile; Francisco J. Ovalle; Cretaceous. Syntypes, SGO.PI.39 (n = 1); SGO.PI.4582 (n = 1).
- dunkeri*, *Natica* – Philippi, 1851b: 44–45; 1853c: 144–145, pl. 19, fig. 19. Locality un-



- known; Dunker coll. Holotype, ZMB 101960 (Kabat & Kiliyas, 1991: 320).
- elegans*, *Cryptostoma* – Philippi, 1841f: 20; 1844z4: 20, 54, [87], as *Sigaretus* (*Cryptostoma*), pl. 3, fig. 24, *non Sigaretus elegans* Blainville, 1827. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Sinum* (*Sinum*) *subelegans* (d'Orbigny, 1852) (Janssen, 1978b: 194–195, who dated Philippi's species from 1843). Speyer (1870a: 81–82, pl. 12, fig. 12) rejected d'Orbigny's name on the grounds that it "is too ugly" [ist zu unschön] for this species, and proposed *Sinum philippi*, as Speyer thought the name should recognize its discoverer. Anderson (1960b: 86–87, pl. 3, fig. 1) and Janssen (1978a: 89) used *Sinum philippii* (Speyer, 1870), as the next available name for Philippi's species, but it is a junior synonym of d'Orbigny's name. Type material lost (R. Janssen, pers. comm., April 2013).
- eurymphala*, *Natica* – Philippi, 1887a: 86 [1887b: 81], pl. 9, fig. 21. Isla Quiriquina, Chile; Cretaceous. Syntype, SGO.PI.27 (n = 1, labeled as "paralectotipo?"). *Gyrodus euryomphala* (Philippi, 1887) (Wilckens, 1904: 194–195, 198–200, pl. 17, fig. 10; Wetzel, 1930: 66); *Gyrodus* (*Dockeryella*) *eurymphalus* (Philippi, 1887), Maastrichtian (Bandel & Stinnesbeck, 2000: 765–766, pl. 1, fig. g).
- exilis*, *Natica* – Philippi, 1887a: 90 [1887b: 84], pl. 9, fig. 26. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.28.
- famula*, *Natica* – Philippi, 1887a: 89–90 [1887b: 84], pl. 10, fig. 13a, 13b. Navidad, Chile, & Lebu, Chile; Ramón Vidal Gormáz; Tertiary. Syntypes, SGO.PI.41 (n = 1, from Navidad, labeled as "lectotipo"); SGO.PI.65 (n = 2, from Lebu); SGO.PI.4593–4605 (labeled as "paralectotipo"). *Polinices famula* (Philippi, 1887) (Ihering, 1907: 158–159, 341, pl. 5, fig. 20).
- ferrieri*, *Natica* – Philippi, 1887a: 86 [1887b: 81], pl. 10, fig. 20. Isla Quiriquina & Tumbez, Chile; Cretaceous. Holotype, SGO.PI.6.
- filosa*, *Natica* – Philippi, 1845s: 42 [8], pl. 2, fig. 4, *nom. nov. pro Natica lineolata* Philippi, 1844n, *non* Deshayes, 1832; 1850r: pl. 11, fig. 9; 1852c: 72–73. The Mediterranean *Tectonatica filosa* (Philippi, 1845) (Abbott & Dance, 1982: 108, as *Natica*; Sabelli et al., 1990: 170, as *Natica*; Giribet & Peñas, 1997: 49 [11], as "1844").
- galactites*, *Natica* – Philippi, 1851b: 47; 1853c: 138, pl. 19, fig. 10. Southern China; Hohenacker.
- ganae*, *Natica* – Philippi, 1887a: 84 [1887b: 79], pl. 10, fig. 6. Isla Quiriquina, Chile; Cretaceous. Syntypes, SGO.PI.1 (n = 1, labeled as "paralectotipo"); SGO.PI.4579–4580 (n = 1, each labeled as "paralectotipo"); SGO.PI.6426 (n = 1, labeled as "lectotipo"). Synonym of *Ampullina australis* (d'Orbigny, 1838) (Wilckens, 1904: 197–198, pl. 17, figs. 11–12), or *Polinices* (*Polinella*) *ganae* (Philippi, 1887), Maastrichtian (Bandel & Stinnesbeck, 2000: 766–767, pl. 1, figs. h–i).
- globula*, *Natica* – Philippi, 1887a: 87 [1887b: 81], pl. 10, fig. 19. Isla Quiriquina & Algarrobo, Chile; Cretaceous. Syntypes, SGO.PI.52 (n = 2).
- gouldii*, *Natica* – Philippi, 1845g: 77–78; 1851f: pl. 13, fig. 8; 1852c: 89–90. Maine. Synonym of *Euspira pallida* (Broderip & G. B. Sowerby I, 1829).
- grayi*, *Natica* – Philippi, 1852c: 74–75; 1850r: pl. 11, fig. 13. Replacement name for *Natica depressa* Gray, 1839, *non* (Lamarck, 1801) (J. Sowerby, 1812, had transferred "*Ampullaria*" *depressa* Lamarck to *Natica*). No type locality given by Gray; Philippi's material was from Mazatlán, Mexico. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. The Panamic *Naticarius grayi* (Philippi, 1852) (Keen, 1971: 474–475, fig. 863, as *Natica*; Marincovich, 1977: 385–387, pl. 37, fig. 12, pl. 40, fig. 1; Ramírez et al., 2003: 260).
- gruneriana*, *Natica* – Philippi, 1852c: 47–48; 1850r: pl. 7, fig. 6. South coast of China. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. In his synonymy, he indicated that this was for the misidentified specimen of *Natica cumingiana* Récluz, 1843, that he had incorrectly figured in the *Abbildungen* (pl. 2, fig. 13).
- hebraea*, *Natica* – Philippi, 1852c: 73; 1850r: pl. 11, fig. 10, *non* (Martyn, 1786). Locality not stated. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. This name is a junior secondary homonym of the common Mediterranean *Natica hebraea* (Martyn, 1786) [ICZN Opinion 1622], which is now usually placed in *Naticarius*.
- hupeana*, *Natica* – Philippi, 1887a: 88–89 [1887b: 83], not figured. Navidad, Chile; J. Toribio Medina; Tubul, Chile, Volckmann; Tertiary. Syntypes, SGO.PI.48 (n = 1, from Tubul, labeled as "lectotipo"); SGO.PI.4583–4589 (n = 1 each, labeled as "paralectotipo").



- impervia*, *Natica* – Philippi, 1845i: 65; 1845s: 42–43 [8–9], pl. 2, fig. 6; 1851f: pl. 13, fig. 11; 1852c: 92. Strait of Magellan, Chile. Type material not found in MNHNS (Pastorino, 2005b: 233). *Tectonatica impervia* (Philippi, 1845) (Dell, 1990: 163–164, 141, fig. 249, 146, fig. 274; Forcelli, 2000: 78, both as *Natica*; Carcelles & Williamson, 1951: 283; Castellanos & Landoni, 1990: 24–25, pl. 3; Pastorino, 2005b: 231–234, all as *Tectonatica*).
- incei*, *Natica* – Philippi, 1853b: 233; 1853c: 142, pl. 19, fig. 15, misspelled as *N. "incci"*. Raines Island, Torres Strait; Capt. Ince; Cuming coll. Misspelled as *N. incii* by Reeve (1855: pl. 20, fig. 89). The Australian *Glossaulax incei* (Philippi, 1853) (Wilson, 1993: 220, pl. 36, fig. 41a, b).
- intermedia*, *Natica* – Philippi, 1836a: xi, 163, 256, pl. 9, fig. 11, *non* Deshayes, 1832. Palermo, Sicily, Italy. Philippi (1836a: 256) concluded that his *N. intermedia* was a synonym of *N. marochiensis* Gmelin, 1791 [as "Lamarck"]. Synonym of *Euspira nitida* (Donovan, 1804) (Sabelli et al., 1990: 171).
- intemerata*, *Natica* – Philippi, 1853b: 233–234; 1853c: 129–130, pl. 18, fig. 10. Gulf of California; Rev. Steel; Cuming coll. *Polinices intemeratus* (Philippi, 1853), Panamic (Keen, 1971: 478–479, fig. 877; Marincovich, 1977: 253–255, pl. 22, figs. 8–9; Ramírez et al., 2003: 260).
- lactea*, *Natica canrena* – Philippi, 1853c: 137–138, pl. 19, fig. 9. Locality not stated. Synonym of the western Atlantic *Naticarius canrena* (Linnaeus, 1758).
- lactea*, *Natica melanostoma* – Philippi, 1852c: 31. Locality not stated. Synonym of *Mammilla melanostoma* (Gmelin, 1791) (Kabat, 2000: 354).
- lemniscata*, *Natica* – Philippi, 1853b: 122, pl. 17, fig. 9. Locality unknown. Holotype, MNHNS 207 (n = 1, 21.4 mm x 19.9 mm). The Japanese *Tanea lemniscata* (Philippi, 1853) (Abbott & Dance, 1982: 106, as "1851" and *Natica*; Higo et al., 1999: 147, as "1852").
- lepida*, *Natica* – Philippi, 1887a: 85 [1887b: 80], pl. 10, fig. 24. Isla Quiriquina, Chile; Cretaceous. Syntype, SGO.PI.31 (n = 1, labeled as "lectotipo").
- lineolata*, *Natica* – Philippi, 1844n: 107–108, *non* Deshayes, 1832. Palermo & Athens, Mediterranean. The Mediterranean *Tectonatica filosa* (Philippi, 1845s), *nom. nov.* (Abbott & Dance, 1982: 108, as *Natica*; Sabelli et al., 1990: 170, as *Natica*; Giribet & Peñas, 1997: 12, as "1844").
- listeri*, *Natica* – Philippi, 1852c: 83; 1850r: pl. 12, fig. 11. Gulf of Mexico. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. Synonym of *Neverita duplicata* (Say, 1822); type material unknown (Hülsken et al., 2006: 16–17, who misdated it as 1851).
- lurida*, *Natica* – Philippi, 1836a: 256, as "*luridam*"; 1850r: pl. 12, figs. 2–4; 1852c: 79–80. Sicily, Italy. Philippi originally (1836a: 256) based this species on the specimen illustrated by Chemnitz (1781: pl. 188, figs. 1907, 1908). Subsequently, Philippi (1852c: 79–80) concluded that it was a synonym of "*Natica maroccana* Chemnitz" (a non-binomial name), for which *N. marochiensis* (Gmelin, 1791) is the first available name for this tropical Atlantic species. Philippi incorrectly recorded this species from both the Atlantic and the Pacific Ocean. Qi (2004: 68, pl. 39B) incorrectly listed *Natica lurida* Philippi, 1852, from China, while Higo et al. (1999: 147) also incorrectly listed *N. lurida* Philippi, 1852, as a synonym of *Natica gualtieriana* Récluz, 1844.
- lynx*, *Natica* – Philippi, 1851b: 46; 1853c: 137, pl. 19, fig. 7. Mangalore, India; R. F. Hohenacker.
- macilenta*, *Natica* – Philippi, 1844g: 140, 141, 302, pl. 24, fig. 14; 1850r: pl. 10, figs. 10, 11; 1852c: 66–[65a]. Naples. Syntypes, PHB Ma Ga. 453 (V) 123 (n = 10; largest, 7.5 mm x 6.4 mm). *Euspira macilenta* (Philippi, 1844) (Sabelli et al., 1990: 170).
- macrostoma*, *Natica* – Philippi, 1852c: 55; 1850r: pl. 9, fig. 1, *non* Römer, 1836. Locality unknown. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. Synonym of *Mammilla melanostomoides* (Quoy & Gaimard, 1832) (Kabat, 2000: 354), or of *Mammilla kurodai* (Iw. Taki, 1943) (Higo et al., 1999: 145). Qi (2004: 67, pl. 39-I) used *Polinices macrostomus* (Philippi, 1852), but the name is preoccupied.
- maculata*, *Natica melanostoma* – Philippi, 1852c: 31. Locality not stated. Synonym of *Mammilla sebae* (Récluz, 1844) (Kabat, 2000: 354).
- martinianus*, *Sigaretus* – Philippi, 1844q: 144–145 [2–3], pl. 1, fig. 5. Locality unknown. Synonym of the western Atlantic *Sinum maculatum* (Say, 1831) (Tunnell et al., 2010: 179).
- maximus*, *Sigaretus* – Philippi, 1844q: 143 [1], pl. 1, fig. 1. Peru. Syntypes, MNHNS 60.181 (n = 2) (fide Marincovich, 1977: 345; not seen



- in March 2014). Synonym of *Sinum cymba* (Menke, 1828), from Ecuador to northern Chile (Marincovich, 1977: 343, 345).
- medinae*, *Natica* – Philippi, 1887a: 90 [1887b: 84], pl. 10, fig. 14. Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.23 (n = 1); SGO.PI.4607 (n = 1).
- melanochila*, *Natica* – Philippi, 1852c: 56–57; 1850r: pl. 9, fig. 2. Locality unknown. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. Synonym of *Mammilla melanostoma* (Gmelin, 1791) (Kilburn, 1976: 865; Kabat, 2000: 354).
- menkeana*, *Natica* – Philippi, 1851b: 45–46; 1851f: pl. 15, fig. 8; 1852c: 106. Puerto Rico; Menke. The western Atlantic *Natica menkeana* Philippi, 1851 (Rios, 1994: 81, pl. 27, fig. 313).
- minor*, *Natica clausa* var. – Philippi, 1852c: 99–100, pl. 14, fig. 6, *non* l. Lea, 1833. Greenland and northeastern United States. Synonym of *Cryptonatica affinis* (Gmelin, 1791) (Bouchet & Warén, 1993: 763–764).
- modesta*, *Natica* – Philippi, 1852c: 113–114; 1851f: pl. 16, fig. 4. Marquesas “?”. The uncaptioned plate (1851) appeared one year before the text (1852) making the name available. Lectotype, ZMB 101966 (designated by Kabat & Kiliyas, 1991: 321) (10.9 mm x 9.9 mm); paralectotype; ZMB 101967 (8.5 mm x 8.2 mm).
- nucleus*, *Natica* – Philippi, 1852c: 107; 1851f: pl. 15, fig. 12. Locality unknown. The uncaptioned plate (1851) appeared one year before the text (1852) making the name available.
- obtecta*, *Natica* – Philippi, 1887a: 88 [1887b: 82–83], pl. 10, fig. 2a, 2b; 1897: pl. 3, fig. 7, pl. 10, fig. 1. Navidad, Matanzas, Lebu (MacSporran), Chiloé (Martin), Santa Cruz, Chile; Tertiary. Syntypes, SGO.PI.21 (n = 4, Matanzas); SGO.PI.22 (n = 1, Lebu); SGO.PI.35 (n = 1, Santa Cruz); SGO.PI.71 (n = 4, Navidad). Griffin & Pastorino (2013: 516, 519) determined that this species was, in part (Philippi’s fig. 2b, from Santa Cruz, Patagonia), a junior synonym of *Glossaulax secundum* (Rochebrune & Mabile, 1885), with the other figured type specimen (Philippi’s fig. 2a) a distinct species.
- obturata*, *Natica* – Philippi, 1855a: 208; 1856c: 100; 1856e: 165. Strait of Magellan. Type material not found in MNHNS (Pastorino, 2005b: 233). Synonym of *Tectonatica impervia* (Philippi, 1845) (Pastorino, 2005b: 231–234).
- oliviformis*, *Natica* – Philippi, 1887a: 84 [1887b: 78], pl. 10, fig. 5. Isla Quiriquina, Chile; Cretaceous. Syntypes, SGO.PI.69 (n = 1, labeled as “lectotipo”); SGO.PI.4578 (n = 1, labeled as “paralectotipo”). *Ampullina australis* (d’Orbigny, 1842) (Wilckens, 1904: 197–198, pl. 17, figs. 11–12). Bandel & Stinnesbeck (2000: 767) stated that *N. oliviformis* “may well represent a variety of” *Polinices (Polinella) ganae* (Philippi, 1887).
- ovoidea*, *Natica* – Philippi, 1887a: 89 [1887b: 84], pl. 10, fig. 10a, 10b. Tubul, Chile; Volckmann & Llancahue, Chile; Wilhelm Frick, both Tertiary. Syntypes, SGO.PI.33 (n = 3, Llancahue); SGO.PI.59 (n = 1, Tubul, labeled as “lectotipo”); SGO.PI.62 (n = 6, Llancahue); SGO.PI.4590 (n = 1, Tubul, labeled as “paralectotipo”). Griffin & Pastorino (2013: 513) determined that subsequent records of this species from Punta Arenas, Patagonia, Chile, were misidentifications for *Polinices puntarenas* Ihering, 1907.
- ovulum*, *Natica* – Philippi, 1887a: 87 [1887b: 81], pl. 9, fig. 25. Tumbez, Chile; Cretaceous.
- pallens*, *Natica* – Philippi, 1849i: 157–158. Mergui Archipelago, Burma [Myanmar]. Synonym of *Natica vitellus* (Linnaeus, 1758), the type species of *Natica* (Wilson, 1993: 217, pl. 36, fig. 28).
- pardalis*, *Natica* – Philippi, 1851b: 46–47; 1851f: pl. 16, fig. 2; 1852c: 112. Locality unknown.
- patagonica*, *Natica* – Philippi, 1845i: 65; 1845s: 41 [7], pl. 2, fig. 2; 1850r: pl. 8, fig. 6; 1852c: 52–53. Strait of Magellan, Chile. Holotype, MNHNS 190 (33.5 mm x 30.7 mm) (Pastorino, 2005b: figs. 84–85). *Euspira patagonica* (Philippi, 1845) (Dell, 1990: 148, 141, fig. 248, as *Falsilunatia*; Forcelli, 2000: 77; Pastorino, 2005b: 242–245; Cárdenas et al., 2008: 212; Griffin & Pastorino, 2013: 507–509).
- pfeifferi*, *Natica* – Philippi, 1851b: 45; 1853c: 139–140, pl. 19, fig. 12. Caribbean; Pfeiffer, Dunker & Philippi colls. Synonym of *Polinices lacteus* (Guilding, 1834) (A. R. Kabat, pers. obs.).
- pisum*, *Natica* – Philippi, 1887a: 90 [1887b: 85], pl. 10, fig. 25. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.24.
- planus*, *Sigaretus* – Philippi, 1844q: 146 [4], pl. 1, fig. 7. Locality unknown. Junior synonym of the Indo-Pacific *Sinum planatum* (Récluz, 1843) (Kilburn, 1976: 874–876).
- plicifera*, *Natica* – Philippi, 1852c: 84–84; 1851f: pl. 12, fig. 13, ex Dunker ms. The uncaptioned plate (1851) appeared one



- year before the text (1852) making the name available. It was credited to Dunker, but there is no indication that he wrote the description. East coast of South Africa. Holotype, ZMB 101968 (23.2 mm x 21.7 mm) (Kabat & Kiliyas, 1991: 321). Junior synonym of the Indo-Pacific *Naticarius alapapilionis* (Röding, 1798) (Kilburn, 1976: 843–844).
- pomum*, *Natica* “?” – Philippi, 1853b: 234; 1853c: 128–129, pl. 18, fig. 9. Locality unknown; Cuming coll. Syntype, NHMUK 20110268. Probably a thin-shelled *Bulbus* or *Euspira* from the northern Atlantic (A. R. Kabat, pers. obs.). Hubendick (1945: 109) determined that several erroneous citations to “*Ampullarina*” *pomum* (classified in the Amphibolidae) were to this species of Naticidae.
- ponderosa*, *Natica* – Philippi, 1852c: 32–33; 1849z4: pl. 4, figs. 9, 10; 1853c: 125, pl. 18, figs. 4, 5. Locality unknown. The uncaptioned plate (1849) appeared three years before the text (1852) making the name available. Kilburn (1976: 856–857) treated this as a junior synonym of *P. tumidus* (Swainson, 1840), which is now regarded as a junior synonym of *P. mammilla* (Linnaeus, 1758). Synonym of the western Pacific *Polinices mammilla* (Linnaeus, 1758) (Kabat, 1990: 16–19, fig. 3A, B; Wilson, 1993: 220, pl. 36, fig. 30; Higo et al., 1999: 144).
- puella*, *Natica* – Philippi, 1852c: 64–65; 1850r: pl. 10, fig. 7. Yucatan; Largilliert. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available text. Synonym of *Polinices lacteus* (Guilding, 1834) (A. R. Kabat, pers. obs.).
- pulicaris*, *Natica* – Philippi, 1852c: 90–91; 1851f: pl. 13, fig. 9. Locality unknown. The uncaptioned plate (1851) appeared one year before the text (1852) making the name available. The Arabian Gulf *Natica pulicaris* Philippi, 1852 (Bosch & Bosch, 1989: 50; Bosch et al., 1995: 86).
- pullus*, *Sigaretus* – Philippi, 1887a: 92 [1887b: 86], pl. 9, fig. 20. Navidad, Chile; Tertiary [Miocene]. *Sinum pullum* (Philippi, 1887), late Miocene to early Pliocene (Griffin & Nielsen, 2008: 307).
- pygmaea*, *Natica* – Philippi, 1842d: 17 [5], pl. 1, fig. 12; 1851f: pl. 13, fig. 12; 1852c: 93. Locality unknown. *Natica pygmaea* Philippi, 1842, from India. Kilburn (1976: 837–838) questioned whether this species was known from South Africa, and used *Natica forata* Reeve, 1855, as the name to be used for prior South African records identified as *N. pygmaea*.
- remondi*, *Natica* – Philippi, 1887a: 85 [1887b: 79–80], pl. 10, fig. 11. Tumbez, Francisco J. Ovalle; Cretaceous. Syntype, SGO.PI.70 (n = 1, labeled as “lectotipo”); SGO.PI.4609 (n = 1, labeled as “paralectotipo”).
- rhodostoma*, *Natica* – Philippi, 1842d: 16 [4], pl. 1, fig. 7. Locality unknown. Synonym of the Indo-Pacific *Tectonatica violacea* (G. B. Sowerby I, 1825) (Wilson, 1993: 219).
- rizzae*, *Natica* – Philippi, 1844n: 108; 1845s: 42 [8], pl. 2, fig. 5; 1851f: pl. 15, fig. 7; 1852c: 105–106. Palermo, Italy. The holotype of *Natica settepassi* Gaglioli in Settepassi, 1985, housed in the Museo di Zoologia, Rome, was designated as the neotype of Philippi’s species by Bouchet & Warén (1993: 764–765), in order to resolve the status of these two species, given that Philippi’s name had been treated as a *nomen dubium* by Moran et al. (1989: 38). *Tectonatica rizzae* (Philippi, 1844) (Bouchet & Warén, 1993: 764–766, figs. 1794, 1822–1823, 1841–1842, 1879, 1895–1896, 1908).
- rodatzii*, *Natica* – Philippi, 1852c: 83–84; 1850r: pl. 12, fig. 12, ex Dunker ms. West coast of South Africa; Capt. Rodatz. This species was noted as being “in litt.”, so Philippi is here credited as being its author. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. Lectotype, ZMB 101974 (23.9 mm x 21.2 mm) (designated by Kabat & Kiliyas, 1991: 322); paralectotypes ZMB 101975 (n = 2). Kilburn (1976: 857) thought that this species belonged in *Neverita* or *Polinices*, but questioned the type locality: “In all probability the type-specimen came from further north (the collector, Captain Rodatz, is known to have visited and collected at Zanzibar).” Kabat & Kiliyas (1991: 322) noted that the specimens from Dunker’s collection came from the Red Sea, collected by Rodatz. *Natica rodatzii* Schepman, 1901, ex Dunker ms., from “Red Sea” is a junior homonym, and probably a junior synonym of the amphiatlantic *Polinices lacteus* (Guilding, 1834) (Mienis, 1992).
- rotelloides*, *Trochus* – Philippi, 1887a: 99 [1887b: 94], pl. 11, fig. 24. Insel Quiriquina, Chile; Cretaceous. Holotype, SGO.PI.808. Wilckens (1904: 194–195, 198–200, pl. 17, fig. 10) concluded that this might be a synonym of *Gyrodes euryomphala* (Philippi, 1887).



*scutulata*, *Natica* – Philippi, 1852c: 119; 1851f: pl. 17, fig. 3. Locality unknown. The uncaptioned plate (1851) appeared one year before the text (1852) making the name available.

*subfasciata*, *Natica melanostoma* – Philippi, 1852c: 31. Locality not stated. Synonym of *Mammilla sebae* (Récluz, 1844) (Kabat, 2000: 354).

*subpicta*, *Natica melanostoma* – Philippi, 1852c: 31. Locality not stated. Synonym of *Mammilla melanostomoides* (Quoy & Gaimard, 1832) (Kabat, 2000: 354).

*sulcosa*, *Natica* – Philippi, 1852c: 76–77; 1850r: pl. 11, fig. 15, *non* MacClelland, 1841 (fossil, India). West coast of Mexico or South America. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. *Natica (Stigmaulax) elenae* Récluz, 1844 (Marincovich, 1977: 402–404, pl. 40, figs. 8–9).

*swainsoni*, *Natica* – Philippi, 1852c: 95–96; 1851f: pl. 14, fig. 1. Locality unknown. The uncaptioned plate (1851) appeared one year before the text (1852) making the name available.

*tessellata*, *Natica* – Philippi, 1849i: 158; 1850r: pl. 7, fig. 7; 1852c: 48–49. Locality unknown. Synonym of *Natica gualtieriana* (Récluz, 1844) (Wilson, 1993: 216, pl. 36, fig. 25; Higo et al., 1999: 147; Kabat, 2000: 354).

*texasiana*, *Natica* – Philippi, 1849i: 158–159; 1849z4: pl. 5, fig. 3; 1849z5: 457; 1851f: pl. 12, fig. 10 (“var.”); 1852c: 37–38, 82–83. Galveston, Texas; Roemer. Synonym of *Neverita delessertiana* (Récluz, 1843); type material unknown (Hülsken et al., 2006: 18–19).

*undata*, *Natica* – Philippi, 1844g: 141, 302, pl. 24, fig. 16 [*non Natica undata* Philippi, 1852c, from Panama]. Palermo, Sicily, Italy; fossil.

*undata*, *Natica* – Philippi, 1852c: 74; 1850r: pl. 11, fig. 12, *non* Philippi, 1844. [West coast of] Panama; E. B. Philippi. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. *Natica undata* Philippi, 1852 (Dall, 1909: 235; Ramírez et al., 2003: 260), but not noted by either to be a junior homonym of *N. undata* Philippi, 1844. Synonym of *N. chemnitzii* Pfeiffer, 1840, from the eastern Pacific (Marincovich, 1977: 372–374, pl. 36, figs. 10–12).

*venustula*, *Natica* – Philippi, 1851b: 48; 1853c: 145–146, pl. 19, fig. 20. Locality unknown.

*vesicalis*, *Natica* – Philippi, 1849i: 159–160; 1849z4: pl. 6, fig. 1; 1852c: 40–41. Canton,

China; Gruner. The Indo-Pacific *Glossaulax vesicalis* (Philippi, 1849) (Higo et al., 1999: 145; Okutani, 2000: 254–255, fig. 23, as “1848”). Kilburn (1976: 860) had treated it as a junior synonym of *G. didyma* (Röding, 1798).

*vestalis*, *Natica* – Philippi, 1853b: 234; 1851f: pl. 18, fig. 6; 1853c: 126. The uncaptioned plate (1851) appeared two years before the text (1853) making the name available. Mozambique; Rev. Steel; Cuming coll. Kilburn (1976: 856–857) treated this as the “broad form” of *P. tumidus* (Swainson, 1840), which is now regarded as a junior synonym of the Indo-Pacific *P. mammilla* (Linnaeus, 1758) (Kabat, 1990: 16–19).

*vidali*, *Natica* – Philippi, 1887a: 91 [1887b: 85–86], pl. 10, fig. 17. Santa Cruz, Chile; Ramón Vidal Gormáz; Tertiary. Syntypes, SGO.PI.50 (n = 1, labeled as “lectotipo”); SGO.PI.4606, 4608 (n = 1 each, labeled as “paralectotipo”). Griffin & Pastorino (2013: 516, 519) determined that this species was a junior synonym of *Glossaulax secundum* (Rochebrune & Mabile, 1885).

*virginea*, *Natica* – Philippi, 1852c: 81; 1850r: pl. 12, fig. 7. Locality unknown. The uncaptioned plate (1850) appeared two years before the text (1852) making the name available. Synonym of the western Pacific *Polinices flemingianus* (Récluz, 1844) (Wilson, 1993: 222; Higo et al., 1999: 144).

*volckmanni*, *Natica* – Philippi, 1887a: 89 [1887b: 83], pl. 10, fig. 4. Tubul, Chile; Volckmann; Tertiary. Holotype, SGO.PI.19.

*zonata*, *Natica melanostoma* – Philippi, 1852c: 31. Locality not stated. Synonym of the Indo-Pacific *Mammilla melanostoma* (Gmelin, 1791) (Higo et al., 1999: 145; Kabat, 2000: 354).

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“*chemnitzii*, *Natica*” – This name, as “1852”, was listed in the synonymy of *Natica vitellus* (Linnaeus, 1758) by Wilson (1993: 217) and credited to Philippi, but it was first made available by Récluz, 1843 (which itself is a junior homonym but not a junior synonym of the eastern Pacific *N. chemnitzii* Pfeiffer, 1840; Kabat et al., 1997: 18).

“*globosa*, *Natica*” – Philippi, 1850r: 21–22. This name, as “1855”, was listed in the synonymy of *Natica vitellus* (Linnaeus, 1758) by Wilson (1993: 217) and by Higo et al. (1999: 146). However, it was first made available by Anton (1838: 31).



*“magellanica, Natica”* – Hombron & Jacquinot (1848: 64, pl. 16, figs. 28, 29) and Rousseau (1854: 64) credited this name to Philippi. However, Philippi (1855a: 206) explained that he had never described a *“Natica magellanica”*. Pastorino (2005b: 242, 245) concluded that Hombron & Jacquinot and Rousseau had mistakenly written *“Natica magellanica”* when they meant *Natica patagonica* Philippi, 1845.

*“oppleta, Natica”* – Möricke, 1896: 556–557 (*“Natica obtecta”* oder [or] *oppleta* Philippi). It cannot be determined why Möricke listed this alternate spelling for *N. obtecta*.

*“perspicuus, Sigaretus”* – Philippi, 1836a: xi, 165, pl. 10, fig. 5a–c. As “mihi” for a transfer of *Helix perspicua* Linnaeus, 1758, to *Sigaratus*.

*“sordida, Natica”* – Philippi, 1844g: 139. This has been listed as a Philippi species by some authors, sometimes misdated as 1836, and as a synonym of *Euspira fusca* (Blainville, 1825). However, this was merely a misidentification of *Natica sordida* Swainson, 1821 (Priolo, 1963: 33–35 [469–471]).

#### Pterotracheidae

*hippocampus, Pterotrachaea* – Philippi, 1836a: xiii, 242–243; 1844g: 204, 303, pl. 28, fig. 16. Palermo. *Pterotrachaea hippocampus* Philippi, 1836 (Sabelli et al., 1990: 177; Okutani, 2000: 296–297, fig. 2; Seapy, 2000: 99–115).

#### Rissoidae sensu latu

*antarctica, Hydrobia* – Philippi, 1868: 224. Strait of Magellan, Chile; William Acton. Valdovinos (1999: 129) and Letelier et al. (2003: 66) listed this in the Hydrobiidae, but unlikely to be referable to the Hydrobiidae or the Cochliopidae, and more likely a marine rissoid.

*arata, Rissoa* – Philippi, 1849i: 167. Gabon in Guinea; Largilliert.

*aspera, Rissoa* – Philippi, 1844g: 126–127, footnote, 301, pl. 23, fig. 6. Locality unknown, but presumably Italy. *Alvania aspera* (Philippi, 1844) (Sabelli et al., 1990: 149).

*bidentata, Rissoa* – Philippi, 1845i: 64. Insulae Amicorum [Tonga]. The Indo-Pacific *Zebina* (*Zebina*) *bidentata* (Philippi, 1845) (Severns, 2011: 122–123, fig. 2).

*cancellata, Rissoa* – Philippi, 1844g: 303 (footnote). Replacement name for *Rissoa clath-*

*rata* Philippi, 1844, *non* Gray, *non* Grateloup. However, Philippi’s replacement name was itself a junior homonym several times over, of *R. cancellata* Fréminville, 1814; Lamarck, 1822; and Récluz, 1843. Synonym of *Alvania hispidula* (Monterosato, 1884) (Priolo, 1954a: 80–81 [164–165]; Sabelli et al., 1990: 150). *cancellata, Rissoina* – Philippi, 1847r: 127. Cuba; Pfeiffer. Holotype ZMB 2334. *Rissoina cancellata* Philippi, 1847 (Rios, 1994: 53, pl. 17, fig. 187; Tunnell et al., 2010: 149). Dall (1909: 232) and Ramírez et al. (2003: 259) both recorded this in error from Peru. However, Rolán & Fernández-Garcés (2010: 80–82), after reviewing the type material, concluded that this was a junior synonym of *Rissoina sagraiana* d’Orbigny, 1842.

*carinata, Rissoa* – Philippi, 1836a: xi, 150, pl. 10, fig. 10. Thapsi [Magnisi] Peninsula, Sicily, Italy. *Rissoa costata* (J. Adams, 1796) (Tryon, 1887a: 336).

*chilensis, Rissoa* – Philippi, 1887a: 80 [1887b: 75], pl. 8, fig. 19. Navidad, Chile; Tertiary [Miocene].

*cingulata, Rissoa* – Philippi, 1836a: xi, 152–153; 1844g: 128, 301, pl. 23, fig. 14. Magnisi Peninsula, Sicily, Italy. Syntypes, SMF 304983 (Panormo) (n = 1); ZMB 2326 (Magnisi) (not found in September 2013; “destroyed by Byne’s” disease, Garilli, 2008: 27). *Alvania cingulata* (Philippi, 1836) (Priolo, 1954a: 78 [162]; Sabelli et al., 1990: 149; Garilli, 2008: 25–28, figs. 15–26).

*clathrata, Rissoa* – Philippi, 1844g: 223, 303, pl. 28, fig. 20, 20a, *non* Gray, 1826, *non* Grateloup, 1828. Naples, Italy. Syntypes, MNHNS 176 (n = 2). In a footnote on p. 303, Philippi (1844g) changed the name to *Rissoa cancellata* because of the homonymy, an unfortunate choice because that name was also a junior homonym: of Fréminville, 1814, Lamarck, 1822 (secondary homonym) and Récluz, 1843. Synonym of *Alvania hispidula* (Monterosato, 1884) (Priolo, 1954a: 80–81 [164–165]; Sabelli et al., 1990: 150).

*decorata, Rissoa* – Philippi, 1846i: 97. Lesina, Dalmatia [Hvar, Croatia]; Botteri. The Adriatic *Rissoa* (*Goniostoma*) *decorata* Philippi, 1846 (Verduin, 1985: 110–111, fig. 19; Sabelli et al., 1990: 147); *R. decorata* Philippi, 1846 (Giribet & Peñas, 1997: 48 [10]).

*delicata, Rissoa* – Philippi, 1849t: 34. Red Sea, Aden; Th. Philippi. *Cingula delicata* (Philippi, 1849) (Issel, 1869: 202).

*dictyophora, Rissoa* – Philippi, 1844g: 128, 131, 301, pl. 23, fig. 11. Thapsi Peninsula,



- Sicily, Italy. *Manzonina* (*Alvinia*) *dictyophora* (Philippi, 1844) (Sabelli et al., 1990: 151); *Alvinia dictyophora* (Philippi, 1844) (Amati & Smriglio, 2016: 165–166, figs. 1a–d, 2a–c, 2j, 5b).
- ehrenbergii*, *Rissoa* – Philippi, 1844g: 127, footnote, 301, as fig. “8”, pl. 23, fig. 9. Algis, Cattaro, Italy; Ehrenberg. Synonym, in part, of *Pusillina marginata* (Michaud, 1832) and of *Pusillina diversa* (Nordsieck, 1972) (Sabelli et al., 1990: 153, as *R. “ehrenbergi”*), or a valid species of *Pusillina* (Bouchet et al., 2001: 188).
- elata*, *Rissoa* – Philippi, 1844g: 122, 301, pl. 23, fig. 3. Naples & Taranto, Italy. Synonym of *Rissoa* (*Rissostomia*) *labiosa* (Montagu, 1803) (Verduin, 1982: 165; Sabelli et al., 1990: 148; Kantor & Sysoev, 2005: 64). Type species (OD) of *Elatiella* F. Nordsieck, 1972, which is now regarded as a synonym of *Rissoa* Sars, 1878.
- erythraea*, *Rissoina* – Philippi, 1851c: 93–94. Maksur, Red Sea, Hemprich & Ehrenberg; Aden, Th. Philippi. Syntypes, ZMB 2335 (n = 8) (Red Sea, ex Hemprich & Ehrenberg). Aartsen (1987b) concluded that Philippi’s species is a *nomen dubium*. Sleurs (1993: 111–112) compared this species with both *Rissoina* (*Apataxia*) *cerithiiformis* Tryon, 1887, and *R. (Phosinella) sequenziana* Issel, 1869, but concluded that the absence of type material or an original illustration precluded a definitive identification of Philippi’s name with either; however, the discovery of syntypes in 2013 may now allow a determination of this species.
- fasciata*, *Rissoa calathicus* var. – Philippi, 1844g: 126. Locality presumably Sicily. *Rissoa cimex* var. *fusca* Philippi, 1844 (Bucquoy et al., 1884: 285, pl. 34, figs. 13–14). Synonym of *Alvinia cimex* (Linnaeus, 1758) (Priolo, 1954a: 77 [161]).
- fusca*, *Rissoa calathicus* var. – Philippi, 1844g: 126, as var. “concolore, rufa vel fusca.” Locality presumably Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1884: 285), as *Rissoa cimex* var. *fusca* Philippi, 1844. Synonym of *Alvinia cimex* (Linnaeus, 1758) (Priolo, 1954a: 77 [161]).
- fusca*, *Truncatella* – Philippi, 1841a: 53–54, 59, pl. 5, fig. 5; 1844g: 134, 301, pl. 24, fig. 4. Palermo, Sicily, Italy. Syntypes, SMF 304978 (Panormino) (n = 14); and ZMB 14031 (n = 2); possible syntypes USNM 182936 (Jeffreys, ex Mörch); USNM 182941 (Jeffreys, ex Philippi “Berlin Museum”). Type species (SD Wenz, 1943: 1498) of *Rudolphosetia* Monterosato, 1917, which is now regarded as a synonym of *Setia*. *Cingula* (*Setia*) *fusca* (Philippi, 1841), an uncommon Mediterranean species (Aartsen & Verduin, 1978: 29–30, figs. 2–4; Verduin, 1984: 53–54, fig. 17).
- grandis*, *Rissoina* – Philippi, 1847r: 127. Philippine Islands. Sleurs (1993: 92–94, 99–100) compared this species with both *Rissoina* (*Moerchiella*) *gigantea* (Deshayes, 1848) and *R. (M.) striata* (Quoy & Gaimard, 1833), but concluded that the absence of type material or an original illustration rendered Philippi’s name a *nomen dubium*.
- granulata*, *Rissoa* – Philippi, 1836a: xi, 153. Ognina, Catania, Sicily, Italy. Also fossil. Syntypes SMF 304920 (n = 5) (Sicily & Cetta); SMF 342263 (n = 9) (Sicily); PHB MB Ga. \_\_\_\_ (XI) 10 (n = 2) (Pozzuoli). Synonym of *Alvinia cimex* (Linnaeus, 1758) (Priolo, 1954a: 75–77 [159–161]; Sabelli et al., 1990: 149).
- granulum*, *Rissoa* – Philippi, 1844g: 130, 132, 301, pl. 23, fig. 24. Magnisi Peninsula, Sicily, Italy. *Nomen dubium*; type material not found (Verduin, 1984: 70), or “possibly” a junior synonym of *R. semistriata* Montagu, 1808 (Tryon, 1887a: 352).
- labiata*, *Rissoa* – Philippi, 1836a: xi, 155, pl. 10, fig. 7; 1844g: 127, 131. [Grotto of] Mardolce, Sicily, Italy; fossil. Syntype, PHB MB Ga. 458 (XI) 10 (n = 1) (Mardolce). Synonym of *Alvinia* (*Galeodina*) *carinata* (Da Costa, 1779) (Priolo, 1954a: 81–83 [165–167]).
- lactea*, *Rissoa calathicus* var. – Philippi, 1844g: 126, as var. “concolore, lactea.” Locality presumably Sicily. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1884: 285), as *Rissoa cimex* var. *lactea* Philippi, 1844. Synonym of *Alvinia cimex* (Linnaeus, 1758) (Priolo, 1954a: 77 [161]).
- monodonta*, *Rissoa* – Philippi, 1836a: xi, 151, pl. 10, fig. 9; 1844g: 125, 301, pl. 23, fig. 1 [not cited in text], ex Bivona ms. Philippi also cited “*Rissoa monodonta* Menke”, but this seems to have been an error for *Rissoa mucronata* Menke, 1830, which is on the cited page of Menke’s *Synopsis* (p. 138). There is no earlier *Rissoa monodonta* than that of Philippi. Syntypes, SMF 233473 (n = 9); SMF 304938 (n = 3) (Sicily). Neotype ZMB 80715 (Palermo, ex Monterosato), designated by Verduin (1983: 63, fig. 2a), who was unaware of the syntypes in SMF. ICZN Code Article 75.8 (1999) applies, and the syntype takes



- precedence over the neotype. *Rissoa* (*Loxostoma*) *monodonta* Philippi, 1836 (Verduin, 1983: 61–63; Sabelli et al., 1990: 148); *R. monodonta* Philippi, 1836 (Giribet & Peñas, 1997: 48 [10]). Incorrectly listed by Schwartz von Mohrenstern (1858: 16) as the type species of *Rissoa* Desmarest, 1814, but it was not an originally included species.
- nana*, *Rissoa* – Philippi, 1844z4: 52; 1844g: 127, 131, *nom. nov. pro Rissoa pusilla* Philippi, 1836a, *non* Grateloup, 1828, *non Rissoa pusilla* (Brocchi, 1814). Synonym of *Pusillina philippi* (Aradas & Maggiore, 1844) (Sabelli et al., 1990: 153).
- obscura*, *Rissoa* – Philippi, 1844g: 127, footnote, 301, pl. 23, fig. 10. Locality not stated, but presumably Italy. *Nomen dubium*; type material not found in ZMB (Verduin, 1985: 122). Either a synonym of *Rissoa parva* (Da Costa, 1779) (Priolo, 1954b: 193–195 [184–186]), or a valid species, *Pusillina obscura* (Philippi, 1844) (Kantor & Sysoev, 2005: 64).
- ornata*, *Rissoa* – Philippi, 1846i: 97. Lesina, Dalmatia [Hvar, Croatia]; Botteri. Synonym of *Rissoa splendida* Eichwald, 1830 (Tryon, 1887a: 325, pl. 61, fig. 16).
- pulchella*, *Rissoa* – Philippi, 1836a: xi, 155, pl. 10, fig. 12; 1844g: 127, 131, *non* Risso, 1826. Melitello, Sicily, Italy; fossil [Pleistocene]. Syntypes, SMF 304947 (n = 2) (Magnisi, Sicily); ZMB 2322 (n = 1) (Sicily); PHB MB Ga. \_\_\_\_ (XI) 10 (Melitello) (n = 3); the specimen cited by Verduin (1976a: 42–44) in the Institut Royal des Sciences Naturelles de Belgique is a topotype collected by Monterosato, not a name-bearing type (Y. Samyn, in litt., 18 Nov. 2014). Synonym of *Pusillina diversa* (Nordsieck, 1972) (Verduin, 1976a: 42–44, 69, pl. 5, as *Rissoa*; Sabelli et al., 1990: 153).
- pusilla*, *Rissoa* – Philippi, 1836a: xi, 154, pl. 10, fig. 13, *non* (Brocchi, 1814), *non* Grateloup, 1828, *non* (Marcel de Serres, 1829). Thapsi [Magnisi] Peninsula, Sicily, Italy. Syntypes, SMF 304942 (n = 3) (Magnisi). Three substitute names were proposed: *Rissoa nana* Philippi, 1844z4, *non* Grateloup, 1828; *Rissoa philippi* Aradas & Maggiore, 1844; and *Rissoa dolium* Nyst, 1845. *Pusillina dolium* (Nyst, 1845) (Priolo, 1954a: 195–197 [186–188]; Kantor & Sysoev, 2005: 64), but it should instead be the earlier *Pusillina philippi* (Aradas & Maggiore, 1844) (Aartsen & Giannuzzi Savelli, 1987: 271–272; Sabelli et al., 1990: 153; Bouchet & Warén, 1993: 674; Landau et al., 2013: 69, pl. 6, fig. 2, pl. 56, figs. 5–6). *Rissoa pusilla* Philippi, 1836, is the type species (M) of *Pusillina* Monterosato, 1884.
- radiata*, *Rissoa* – Philippi, 1836a: xi, 151–152, pl. 10, fig. 15; 1844g: 128. Palermo, Sicily, Italy. Syntypes, SMF 233241 (n = 7) (Sicily); SMF 304948 (n = 2) (Palermo); SMF 304950 (n = 3) (Sicily); ZMB 2315. *Pusillina radiata* (Philippi, 1836) (Verduin, 1976a: 34–38, 68–69, pl. 1, figs. 4–7, pl. 2, pl. 3, figs. 1–3, as *Rissoa*; Sabelli et al., 1990: 153; Giribet & Peñas, 1997: 48 [11]). Type species (OD) of *Radiatia* F. Nordsieck, 1972, a synonym of *Pusillina* Monterosato, 1884.
- reticulata*, *Rissoa* – Philippi, 1836a: xi, 156, pl. 10, fig. 14; 1844g: 131. Palermo, Sicily, Italy; fossil. Syntype, PHB MB Ga. 457 (XI) 10 (n = 1). The use of this name for a German Oligocene species by Philippi (1844z4: 73) was in error; the Oligocene records are referable to *Alvania* (*Arsenia*) *multicostata* (Speyer, 1864) (Janssen, 1978a: 39).
- rimata*, *Rissoa* – Philippi, 1844z4: 52, [87], pl. 3, fig. 17. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. *Rissoa* (*Rissoa*) *rimata* Philippi, 1844 (Speyer, 1869: 324–325, pl. 34, figs. 3–4; Janssen, 1978a: 40), or *Rissoa* (*Schwartzia*) *rimata* Philippi, 1844 (Janssen, 1978b: 155–156, pl. 11, fig. 28).
- rudis*, *Rissoa* – Philippi, 1844g: 128, 301, pl. 23, fig. 12. Magnisi [Thapsi] Peninsula, Sicily, Italy. *Alvania rudis* (Philippi, 1844) (Amati et al., 1987; Sabelli et al., 1990: 150; Giribet & Peñas, 1997: 48 [11]). Type species (M) of *Thapsia* Monterosato, 1884, *non* Albers, 1860 [Pulmonata]. *Thapsiella* P. Fischer, 1885, *nom. nov. pro Thapsia* Monterosato, 1884. *Gentileia* Sullioti, 1888, unnecessary additional replacement name.
- rufa*, *Rissoa* – Philippi, 1849i: 167. Gabon in Guinea; Largilliert. Listed with the “doubtful and spurious species” by Tryon (1887a: 368).
- scabra*, *Rissoa* – Philippi, 1844g: 126–127, 301, pl. 23, fig. 8. Thapsi [Magnisi] Peninsula, Sicily, Italy. Syntypes, MNHNS 178 (n = 2). *Alvania scabra* (Philippi, 1844) (Priolo, 1954a: 71–73 [155–157]; Sabelli et al., 1990: 150; Landau et al., 2004: 42–43, pl. 8, fig. 2). Type species (OD) of *Alvaniella* Sacco, 1895, ex Monterosato ms.
- scalarioides*, *Rissoina* – Philippi, 1848b: 13–14, ex H. (?) Adams ms. Cuba, Jamaica, etc., Caribbean. *Rissoina scalarioides* Philippi, 1848 (Faber, 1990: 118).



*schythei*, Rissoa – Philippi, 1868: 225. Strait of Magellan, Chile[; William Acton]. *Onoba schythei* (Philippi, 1868) (Ponder & Worsfold, 1994: 39, 40–43; Valdovinos, 1999: 129; Forcelli, 2000: 71; Letelier et al., 2003: 67, first and third citations as “*O. schytei*”).

*sculpta*, Rissoa – Philippi, 1844g: 131, 301, pl. 23, fig. 21. Apulia & Gravina, Italy; Scacchi; fossil [Plio-Pleistocene]. Synonym of *Alvania cimicoides* (Forbes, 1844) (Fretter & Graham, 1978: 175–176, figs. 151, 152; Bouchet & Warén, 1993: 624–626, figs. 1381–1385). However, Philippi’s name was published first in 1844.

*simplex*, Rissoa – Philippi, 1844g: 129–130, 133, 301, pl. 23, fig. 17. Magnisi Peninsula, Sicily, Italy. Syntype, ZMB 9037 (n = 1). Probably a synonym of *Rissoa radiata* Philippi, 1836 (Verduin, 1976a: 36), now regarded as *Pusillina radiata* (Philippi, 1836) (Sabelli et al., 1990: 153; Giribet & Peñas, 1997: 48 [11]).

*solidula*, Rissoa – Philippi, 1849i: 167. Gabon in Guinea; Largilliert. Listed with the “doubtful and spurious species” by Tryon (1887a: 368).

*soluta*, Rissoa – Philippi, 1844g: 130, 301, pl. 23, fig. 18. Palermo, Sicily, & Sorrento, Italy. *Nomen dubium*; type material not found (Verduin, 1984: 71), or *Setia soluta* (Philippi, 1844) (Sabelli et al., 1990: 154), or as *Cingula* (*Pseudosetia*) *soluta* (Philippi, 1844) (Priolo, 1953b: 185–186 [130–131]).

*substriata*, Rissoa – Philippi, 1844g: 132, 301, pl. 23, fig. 20. Palermo; fossil. *Cingula substriata* (Philippi, 1844) (Verduin, 1984: 60–61, figs. 24, 73), or as *Alvania* (*Crisilla*) *substriata* (Philippi, 1844) (Fasulo & Gaglini, 1987: 19–22, fig. 4).

*subsulcata*, Rissoa – Philippi, 1844g: 129, 301, pl. 23, fig. 16. Palermo, Sicily, Italy. Synonym of *Cingula semistriata* (Montagu, 1808) (Priolo, 1954a: 60–61 [144–145]; Fretter & Graham, 1978: 159–160, fig. 135).

*tenera*, Rissoa – Philippi, 1844g: 128–129, 301, pl. 23, fig. 15. Thapsi Peninsula, Sicily, Italy. *Alvania* (*Galeodina*) *tenera* (Philippi, 1844) (Sabelli, 1990: 151; Garilli, 2008: 39, 41–42, figs. 80–82).

*textilis*, Rissoa – Philippi, 1844g: 131–132, 301, pl. 23, fig. 22. Contrada Carrubara, Calabria, Italy; fossil [Pleistocene]. *Massotia textilis* (Philippi, 1844) (Kantor & Sysoev, 2005: 61), or a synonym of the Recent *Alvania reticulata* (Montagu, 1803) (Priolo, 1954a: 74 [158]).

*umbilicata*, Rissoa – Philippi, 1851c: 93. China; Largilliert. Listed with the “doubtful and spurious species” by Tryon (1887a: 368).

*venusta*, Rissoa – Philippi, 1844g: 124–125, footnote, 301, pl. 23, fig. 4. Venice, Italy. Syntypes, SMF 304941 (n = 4); ZMB 14045 (n = 12). Synonym of *Rissoa* (*Rissostomia*) *labiosa* (Montagu, 1803) (Verduin, 1982: 165; Sabelli et al., 1990: 148) or of *Rissoa membranacea* (J. Adams, 1800) (Kantor & Sysoev, 2005: 64).

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“*desnoyersii*, Rissoa” – Philippi, 1836a: xi, 151. As “mihi” for a transfer of *Paludina desnoyersii* Payraudeau, 1826, to *Rissoa*.

“*fulva*, Rissoa” – Philippi, 1836a: xi, 152. Listed on p. xi as “mihi”, but correctly as of Michaud (1830) on p. 152.

#### Anabathridae

*punctulum*, Rissoa – Philippi, 1836a: xi, 154, p. 10, fig. 11. Thapsi [Magnisi] Peninsula, Sicily, Italy. Synonym of *Pisinna glabrata* (Mühlfeldt, 1824) (Sabelli et al., 1990: 155). Type species (SD Cossmann, 1921) of *Pisinna* Monterosato, 1878.

#### Bithyniidae

*salinesii*, *Paludina* – Philippi, 1844n: 107; 1846w: 137 [11], pl. 2, fig. 11. Palermo; Schultz. Syntypes, SMF 302090 (n = 6) (Panormi). Synonym of *Bithynia* (*B.*) *rubens* (Menke, 1830) (Forcart, 1965: 75).

#### Caecidae

*Odontidium* Philippi, 1836a: ix, 102. Type species (M): *Odontidium rugulosum* Philippi, 1836; = *Caecum trachea* (Montagu, 1803). Synonym of *Caecum* Fleming, 1813.

*rugulosum*, *Odontidium* – Philippi, 1836a: ix, 102, pl. 6, fig. 20a, 20b; 1844g: 73. Thapsi [Thapsos], Peninsula, Magnisi, Sicily, Italy. Syntypes, SMF 304811 (n = 5). Synonym of *Caecum trachea* (Montagu, 1803) (Priolo, 1956b: 228–229 [268–269]; Aartsen, 1977: 13, 17; Sabelli et al., 1990: 156).

#### Tornidae

*carinata*, *Delphinula* – Philippi, 1841f: 21; 1844z4: 11, 55, [87], pl. 3, fig. 26, *non* Woodward, 1833. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. Possible synonym of *Circulus dubius* (Philippi, 1841) (Janssen, 1978b: 159, who dated *D. carinata* from 1843); Anderson (1959: 61–62, pl. 3,



- figs. 5a–c) and Janssen (1978a: 43) used *Circulus carinatus* (Philippi, “1843”), with *Delphinula dubia* a junior synonym. Type material lost (R. Janssen, pers. comm., April 2013).
- dubia*, *Delphinula* – Philippi, 1841f: 21; 1844z4: 21, 55, [87], pl. 3, fig. 28. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Circulus dubius* (Philippi, 1841) (Janssen, 1978b: 159, pl. 11, figs. 35–36), or a synonym of *Circulus carinatus* (Philippi, 1841) (Speyer, 1869: 317–318; Anderson, 1959: 61–62, pl. 3, figs. 5a–c; Janssen, 1978a: 43, both as “1843”), but the latter name is a junior homonym. Type material lost (R. Janssen, pers. comm., April 2013).
- scaber*, *Adeorbis* – Philippi, 1849h: 127; 1853e: 4–5, pl. 1, fig. 2. Panama; E. B. Philippi. The Panamic *Macromphalina scabra* (Philippi, 1849) (Keen, 1971: 454).
- striata*, *Valvata* – Philippi, 1834b: 520 [*nomen nudum*]; 1836a: xi, 147, pl. 9 [not “8” as in text], fig. 3a–c; 1844g: 122; 1844z3: [3]. Cefali, Catania, Sicily, Italy; fossil. *Circulus striatus* (Philippi, 1836) (Iredale, 1911: 259–260; Priolo, 1953a: 106–107 [104–105]; Anderson, 1959: 64–65, pl. 3, figs. 8a–b; Janssen, 1967: 127; Adam & Knudsen, 1969: 9–13, figs. 4–5; Fretter & Graham, 1978: 227–228, fig. 190; Sabelli et al., 1990: 155; Giribet & Peñas, 1997: 48 [11]; Haszprunar, 2014: 99).

#### Truncatelloidea (Freshwater)

Note: the South American taxa of “*Hydrobia*” and “*Paludina*” are mostly in the Cochliopidae, and the Australian taxa are mostly in the Tateidae.

- atacamensis*, *Paludina* (*Hydrobia*) – Philippi, 1860a: 185 [1860b: 166], Zool. pl. 7, fig. 15. Tilopozo, Chile. *Heleobia atacamensis* (Philippi, 1860), from Chile (Hershler & Thompson, 1992: 50; Collado et al., 2013: 10).
- atomaria*, *Paludina* – Philippi, 1846w: 136 [10], pl. 2, fig. 6, ex Megerle von Mühlfeld ms. Pará, Brazil.
- coquimbana*, *Paludina* (*Hydrobia*) – Philippi, 1887a: 79 [1887b: 74], pl. 8, fig. 18. Coquimbo, Chile; Quaternary. Junior synonym of *Littoridina* [or *Heleobia*] *australis* (d’Orbigny, 1835) (Aguirre & Farinati, 2000: 579, 583).
- fontinalis*, *Paludina* – Philippi, 1846w: 136 [10], pl. 2, fig. 9. Ohio, U.S.A. Synonym of

- Somatogyrus integra* (Say, 1829) (Walker, 1918: 144).
- preissii*, *Paludina* – Philippi, 1846w: 137 [11], pl. 2, fig. 12. Australia; Preiss. *Tatea preissii* (Philippi, 1846), from Western Australia (Chalmer et al., 1976: 392, 399).
- sinistrorsa*, *Paludina rubens* – Philippi, 1844n: 107. Presumably Sicily, Italy.
- terebellum*, *Rissoa* – Philippi, 1844z4: 52, [87], pl. 3, figs. 19, 19a. Tertiary of Freden & Dieckholz, Niedersachsen, Germany [Late Oligocene]. *Goergesia terebellum* (Philippi, 1844) (Anderson, 1960a: 18, pl. 2, fig. 2; Janssen, 1978b: 165, pl. 12, fig. 40; Rust, 1999: 20). Type species (OD) of *Goergesia* Anderson, 1960, referred to the Hydrobiidae (Pyrgulinae) by Kabat & Hershler (1993: 25).

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- “*francisci*, *Paludina*” – Philippi, 1844j: 117 [5], pl. 1, fig. 15. This was listed by Sherborn (1926: 2508) as if it were a Philippi species, but, as Philippi made clear, it was made available by W. Wood (1828) as *Turbo francesii*, which Philippi misspelled (Coan & Petit, 2011: 37).
- “*kraussiana*, *Paludina*” – Sherborn (1927: 3326) erroneously listed this species as of Philippi, but the article involved was by Dunker (1846: 168–169), without any species attributed to Philippi.

#### Truncatellidae

- “*truncata*, *Rissoa*” – Philippi, 1836a: xi, 151. As “*mihi*” for a transfer of *Paludina truncata* Payraudeau, 1826, to *Rissoa*. Payraudeau’s name, in turn, is an unnecessary new name for *Cyclostoma truncatulum* Draparnaud, 1801, a junior synonym of *Truncatella subcylindrica* (Linnaeus, 1767), the type species, through synonymy, of the genus *Truncatella* Risso, 1826.

#### Strombidae

- medinae*, *Conus* – Philippi, 1887a: 36 [1887b: 33], pl. 1, fig. 6. Navidad, Chile; J. Toribio Medina; Tertiary [Late Miocene]. *Strombus* (*Austrombus*) *medinae* (Philippi, 1887); holotype lost; SGO.PI.5964, neotype (Matanzas) (Nielsen, 2005: 1121–1123, fig. 2.1–2.3); type species (OD) of *Austrombus* Nielsen, 2005.
- ponderosus*, *Strombus* – Philippi, 1842b: 7 [1], pls. 1, 2. Pacific Ocean. Synonym of the Indo-Pacific *Thersistrombus thersites*



(Swainson, 1823) (Abbott, 1960: 55–56, pl. 17, figs. 1, 2; Wilson, 1993: 159, pl. 20, fig. 12; Higo et al., 1999: 109), which is the type species (OD) of *Thersistrombus* Bandel, 2007.

#### Aporrhaidae

*Cerycium* – Philippi, 1841f: 24. Type species (M): *Cerycium paradoxum* Philippi, 1841, = *Strombites speciosus* Schlotheim, 1820. Oligocene, Germany. Note that when Philippi reprinted this publication with additional text (1844z4: 24), he edited the genus name on page 24 to *Chenopus* Philippi, 1836. See the discussion under *Cerycium paradoxum* Philippi, 1841, *infra*.

*Chenopus* – Philippi, 1836a: xiii, 214–216; 1844g: 184–185. Type species (SD Cossmann, 1904): *Strombus pespelecani* Linnaeus, 1758. Objective synonym of *Aporrhais* da Costa, 1778.

*araucanus*, *Chenopus* – Philippi, 1887a: 35 [1887b: 31], pl. 1, fig. 1. Lebu, Chile; Francisco Javier Ovalle; Tertiary [probably Eocene]. Syntypes, SGO.PI.763, SGO.PI.4500–4508 (Nielsen, 2005: 1123, fig. 2.4, 2.5, 2.9). Type species (M) of *Hemichenopus* Steinmann & Wilckens, 1908. *Hemichenopus araucanus* (Philippi, 1887) (Steinmann & Wilckens, 1908: 79–81, pl. 7, fig. 4).

*decussatus*, *Chenopus* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 75, pl. 10, fig. 13. Magdeburg area, Germany; Tertiary; Sack's collection [presumably fossil from Germany].

*desciscens*, *Chenopus* – Philippi, 1844g: 185, 303, pl. 27, fig. 7. Palermo, Sicily, & Lamati, Calabria, Italy; fossil.

*fenestratus*, *Chenopus* “?” – Philippi, 1887a: 35 [1887b: 31], pl. 1, fig. 2. Isla Quiriquina, Chile; Tertiary. Holotype, SGO.PI.764. *Chenopus fenestratus* (Philippi, 1887) (Wilckens, 1904: 204, pl. 18, fig. 4).

*paradoxum*, *Cerycium* – Philippi, 1841f: 24–25; 1844z4: 24–25, 61, 76, [87], pl. 4, fig. 13, as *Chenopus*. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. Type material lost (R. Janssen, pers. comm., April 2013). Synonym of *Drepanocheilus* (*Arrhoges*) *speciosus* (Schlotheim, 1820) (Janssen, 1978a: 82, 1978b: 191–192, who dated Philippi's species from 1843). However, because Philippi's *Cerycium* is available and dates from 1841, it predates both *Drepanocheilus* Meek, 1864, and *Arrhoges* Gabb, 1868.

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“*pesgraculi*, *Chenopus*” – Philippi, 1836a: xiii, 215. As “*mihi*” for the transfer of *Rostellaria pesgraculi* Bronn, 1827, to *Chenopus*.

“*pespelecani*, *Chenopus*” – Philippi, 1836a: xiii, 215. As “*mihi*” for the transfer of *Strombus pespelecani* Linnaeus, 1758, to *Chenopus*.

#### Struthiolariidae

*chilensis*, *Struthiolaria* – Philippi, 1887a: 36 [1887b: 32–33], pl. 1, fig. 4. Matanzas & Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.834 (figured specimen, from Matanzas, labeled as “lectotipo”), SGO.PI.4512–4516 (all from Matanzas). Parodiz (1996: 226) stated that the Ihering collection (now in MACN) contained a specimen of this species “labeled by Ihering as ‘cotypo,’ from Matanzas ... received from R. A. Philippi.” *Perissodonta chilensis* (Philippi, 1887) (Covacevich et al., 1993: 148, 150, pl. 1, figs. 3, 4, as *Struthiolaria*; Nielsen, 2005: 1126–1128, fig. 4.4–4.8).

#### Tonnidae (+ Cassidae)

*affinis*, *Cassis* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 76, pl. 10, fig. 11. Osterweddingen, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene; Hallisches Museum. Synonym of *Cassis ambigua* (Solander in Brander, 1766) (Koenen, 1889: 247–250, pl. 22, figs. 1–3).

*amphora*, *Dolium* – Philippi, 1849c: 12 [6], unfigured. Locality unknown. *Nomen dubium* (Vos & Terryn, 2007: 102).

*ampullaceum*, *Dolium* – Philippi, 1845w: 147; 1849c: 11 [5], pl. 2. Pacific Ocean. The Indo-Pacific *Tonna ampullacea* (Philippi, 1845) (Vos & Terryn, 2007: 60–61, pls. 18–20).

*crenulatum*, *Dolium* – Philippi, 1845w: 148; 1847z: 35–36 [1–2], pl. 1, fig. 1. Caribbean. Synonym of the Indo-Pacific *Tonna zonata* (Green, 1830) (Vos & Terryn, 2007: 66–67, pls. 29, 30).

*depressa*, *Cassidaria* – Philippi, 1844g: 186, 303, pl. 27, fig. 3. Sicily, Italy. Synonym of *Galeodea tyrrhena* (Bruguière, 1792) (Sabelli et al., 1990: 173).

*germari*, *Cassis* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 75, pl. 10a, fig. 10, 10a. Westeregeln; Tertiary; Hallisches Museum. *Cassis germari* Philippi, 1847 (Koenen, 1889: 250–252, pl. 22, figs. 4–5).

*kieneri*, *Dolium* – Philippi, 1847z: 36–37 [2–3], pl. 1, fig. 2. Locality unknown. Synonym of



the Indo-Pacific *Tonna variegata* (Lamarck, 1822) (Vos & Terryn, 2007: 102–103, pls. 50–52).

*marginatum*, *Dolium* – Philippi, 1845w: 147–148. Pacific Ocean. *Nomen dubium* (Vos & Terryn, 2007: 39).

*megacephala*, *Pyrula* – Philippi, 1841f: 26; 1844z4: 26, [87], pl. 4, fig. 18; 1845z: 450. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Cassidaria megacephala* (Philippi, 1841) (Janssen, 1978b: 198–199, pl. 14, fig. 87, who dated the species from 1843). Speyer (1863: 162, 164–165) thought that Philippi's description was inaccurate, and he incorrectly treated it as a synonym of *Cassidaria buchii* Boll, 1851, which is actually the junior name. Type material lost (R. Janssen, pers. comm., April 2013).

*striata*, *Cassis texta* – Philippi, 1836a: 217. Synonym of *Phalium saburon* (Bruguière, 1792) (Sabelli et al., 1990: 173).

*varicosa*, *Cassis texta* – Philippi, 1836a: 217, as var. “adulta, laevis, varicosa.” Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1882: 65), as *Cassis* (*Semicassis*) *saburon* var. *varicosa*.

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“*haemastomum*, *Dolium*” – Philippi (1847w: 147) misspelled *Dolium melanostomum* Jay, 1839 as “*haemastomum*” but subsequently spelled it correctly (Philippi, 1849c: 5–6 [11–12]). Bayer (1937: 50) erroneously listed this as “*D. haemastomum* Philippi, nom. nud.” without recognizing that this was merely a misspelling of Jay's 1839 species.

#### Personiidae

*ringens*, *Tritonium* – Philippi, 1887a: 56–57 [1887b: 53], pl. 4, fig. 9. Navidad & Matanzas, Chile; Tertiary. Syntypes, SGO.PI.744 (figured syntype); SGO.PI.739 (n = 2); SGO.PI.742 (n = 2, Navidad); SGO.PI.4558 (n = 1). *Distorsio ringens* (Philippi, 1887), Oligocene to Miocene (Beu, 2010a: 95–97, pl. 20, figs. 1–5, 7).

*thersites*, *Tritonium* – Philippi, 1887a: 56 [1887b: 53], pl. 4, fig. 8. Ancud, Chile. *Distorsio thersites* (Philippi, 1887); Miocene (Frasinetti, 2006: 66). Lectotype, SGO.PI.840 (Ranquil), designated by Beu (2010a: 96); paralectotypes, SGO.PI.740 (n = 2, Chiloé Island); paralectotypes, SGO.PI.4557 (n = 2, Ranquil; one specimen is actually a *Sassia* species). *Distorsio ringens* (Philippi, 1887),

Oligocene to Miocene (Beu, 2010a: 95–97, pl. 20, figs. 1–5, 7).

#### Ranellidae

*exiguum*, *Tritonium* – Philippi, 1887a: 57 [1887b: 54], pl. 3, fig. 23. Navidad, Chile; Tertiary [Miocene]. Lectotype, SGO.PI.4567 (Navidad), designated by Beu (2010a: 206); paralectotypes, SGO.PI.743, SGO.PI.4565 and SGO.PI.4566 (n = 3), “are all small, juvenile specimens of *Ameranella verruculosa* (G. B. Sowerby I, 1846)” (Beu, 2010a: 206). The lectotype makes Philippi's species a synonym of *Sassia armata* (Hupé, 1854); Oligocene to Miocene, Chile and Argentina (Beu, 2010a: 205–206).

*rugosum*, *Tritonium* – Philippi, 1841f: 27; 1844z4: 27, [87], pl. 4, fig. 25. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. Synonym of *Charonia* (*Sassia*) *flandrica* (Koninck, 1837) (Janssen, 1978b: 199–200). Type material lost (R. Janssen, pers. comm., April 2013).

*tortuosum*, *Tritonium* – Philippi, 1844z4: 60–61, [87], pl. 4, fig. 24, *non Murex tortuosum* Borsson, 1821 (secondary homonym). Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. Renamed *Tritonium philippi* Beyrich, 1854. Type material in PHB MB Ga. \_\_\_\_ (R. Janssen, in litt., 9 Feb. 2016). Synonym of *Charonia* (*Sassia*) *flandrica* (Koninck, 1837) (Janssen, 1978b: 199–200).

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“*wiegmanni*, *Fusus*” – Dall (1909: 285) listed this as a Philippi species, and transferred it to *Cymatium*. However, this was Dall's error for *Fusus wiegmanni* Anton, 1838, now classified in *Monoplex*.

#### Vermetidae

*convolvulus*, *Vermetus* – Philippi, 1887a: 97 [1887b: 92], pl. 11, fig. 27. Navidad, Chile; Tertiary [Miocene]. Vermetidae (Bieler & Petit, 2011: 31).

*laevigatus*, *Vermetus* – Philippi, 1887a: 97 [1887b: 92], not figured. Navidad, Chile; Tertiary [Miocene]. Vermetidae? (Bieler & Petit, 2011: 43).

*maximus*, *Vermetus* – Philippi, 1887a: 97 [1887b: 92], pl. 11, fig. 17. Navidad, Chile; Tertiary [Miocene]. Vermetidae (Bieler & Petit, 2011: 46).

*turbinata*, *Serpula* – Philippi, 1847-l: 80, pl. 10a, fig. 14. Lattorf, Oligocene. Mörch (1861: 149)



transferred this from the Polychaeta to the Vermetidae, as *Burtinella turbinata*. Koenen (1891: 728–729, 743–744, pl. 52, figs. 8–9), as *Vermetus turbinatus* (Philippi, 1847).

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“*gigas*, *Serpulorbis*” – H. & A. Adams, 1854: 359, pl. 39, figs. 2, 2a (among other authors), listed this as a Philippi species, but this was in error for *Vermetus gigas* Bivona-Bernardi, 1832 (Mediterranean) (Bieler & Petit, 2011: 38).

### Xenophoridae

*caperatus*, *Xenophorus* – Philippi, 1849h: 100; 1851e: pl. 49, fig. 2; 1855c: 349–350, as *Xenophora caperata*. Locality unknown; A. B. Meyer. Junior synonym of *Xenophora* (X.) *corrugata* (Reeve, 1842), western Indian Ocean (Ponder, 1983: 38–39, figs. 9d, 25a–c, 28f–h, 35; Kreipl & Alf, 1999: 36–37, text-fig. 14, pl. 5, figs. 3–3d).

*chinensis*, *Trochus* – Philippi, 1841e: 8–9; 1851e: pl. 49, fig. 1; 1855c: 348–349, as *Xenophora “sinensis.”* Locality China. *Xenophora* (*Stellaria*) *chinensis* (Philippi, 1841) (Ponder, 1983: 55–56, figs. 10c, 14n, 29c–g, 40; Wilson, 1993: 168, pl. 23, fig. 10; Higo et al., 1999: 119; Kreipl & Alf, 1999: 60–62, text-fig. 34, pl. 19, figs. 17–17b; Okutani, 2000: 202–203, fig. 8; Qi, 2004: 46, pl. 20F).

*helvaceus*, *Xenophorus* – Philippi, 1851b: 44; 1851e: pl. 47, fig. 1; 1855c: 343–344, as *Xenophora helvacea*. China “?”. Synonym of *Xenophora indica* (Gmelin, 1791) (Ponder, 1983: 59–61, figs. 4a–b, 6b, 11a, 12a, 14s, 31c–f, 41; Wilson, 1993: 169, pl. 23, fig. 3a, b, as “1852”; Kreipl & Alf, 1999: 74–76, text-fig. 43, pl. 27, figs. 25–25b).

*scrutarius*, *Trochus* – Philippi, 1841f: 22; 1844z4: 22, 55, 74, [87], pl. 3, fig. 37. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Tugurium* (*Trochotugurium*) *scrutarium* (Philippi, 1841) (Janssen, 1978a: 84–85, 1978b: 191; Gründel, 1997: 4–5, both of whom dated the species from 1843); or *Xenophora* (X.) *scrutarius* (Philippi, 1841) (Tembrock, 1962: 120; Ponder & Cooper, in Ponder, 1983: 72, who dated the species from 1844).

*wagneri*, *Xenophora* – Philippi, 1855c: 345; 1851e: pl. 47, figs. 2, 3. Cochin, China. The uncaptioned plate (1851) appeared four years before the text (1855) making the name available. “Lectotype”, ZMUC, desig-

nated by Ponder (1983: 61, figs. 31e–f), who stated that Philippi’s description was “based on Schubert & Wagner, 1829, pl. 229, figs. 4062a, b, and Reeve 1843, pl. 1, fig. 2”, and designated the “original specimen of Schubert & Wagner’s figure” as the lectotype. Synonym of *Xenophora indica* (Gmelin, 1791) (Ponder, 1983: 59–62; Wilson, 1993: 169, pl. 23, fig. 3a, b; Kreipl & Alf, 1999: 74–76, text-fig. 43, pl. 27, figs. 25–25b).

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“Xenophoridae” – Philippi, 1853a: 185. Name actually first made available by Troschel (1852), although Philippi was mistakenly credited with it under ICZN Opinion 715 (1964), as noted by Bouchet & Rocroi (2001: 177).

“*Xenophorus*” – Philippi, 1849h: 100. Error *pro* *Xenophora* Fischer von Waldheim, 1807.

### Epitoniidae

*amoena*, *Scalaria* – Philippi, 1844z4: 54, [87], pl. 3, fig. 23. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. *Amaea* (*Scalina*) *amoena* (Philippi, 1844) (Janssen, 1978b: 180, pl. 13, fig. 65).

*araucana*, *Scalaria* – Philippi, 1887a: 83 [1887b: 77–78], pl. 9, fig. 16. Tumbez, Chile; Francisco Javier Ovalle; Tertiary. *Scalaria araucana* Philippi, 1887 (Wilckens, 1904: 202–203, pl. 18, fig. 1; Wetzel, 1930: 66).

*coronata*, *Rissoa* – Philippi & Scacchi, in Philippi, 1840a: 68; 1844g: 127, 301, pl. 23, fig. 7. Naples, Italy. Syntype, MNHNS 179 (n = 1). Priolo (1958: 138 [308]) and Sabelli et al. (1990: 182) and Brown & Neville (2015: 57) considered it a junior synonym of *Opalia hellenica* (Forbes, 1844), but they thought that *coronata* had been described in 1844; instead, it is clearly the senior synonym: *Opalia* (*Nodiscala*) *coronata* (Philippi & Sacchi, in Philippi, 1840) (Palazzi, 2002; Cretella et al., 2005: 119).

*gabbi*, *Scalaria* “?” – Philippi, 1887a: 82 [1887b: 77], pl. 9, fig. 14, *nom. nov. pro* *Scalaria chilensis* Gabb, 1861 (Cretaceous, near Concepcion, Chile), *non* d’Orbigny, 1836. *S. gabbi* de Boury, 1913 (Oligocene-Miocene, Dominican Republic), is a junior homonym, and is in current use as *Epitonium gabbi* (de Boury, 1913) (e.g. Woodring, 1928: 397, pl. 31, figs. 11–12, 1959: 183, pl. 38, fig. 17).

*heyseana*, *Melania* – Philippi, 1847-l: 59–60, pl. 10a, fig. 11. Magdeburg area, Germany; Tertiary; Heyse. *Acirsa heyseana* (Philippi,



1847), Oligocene of northern Germany (Koenen, 1891: 801–803, pl. 48, figs. 4–5). *insignis*, *Scalaria* – Philippi, 1844z4: 54, [87], pl. 3, fig. 21, ex Leunis ms. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Possible syntypes, RPMH (Hildesheim) (n = 2) (figured, Rust, 1999: pl. 2, fig. 2). *Cirsotrema* (*Cirsotremopsis*) *insigne* (Philippi, 1844), per ICZN Code Art. 31.2 (1999) (Janssen, 1978a: 75–76, 1978b: 178, pl. 13, fig. 61; Rust, 1999: 21, pl. 2, fig. 2). *leunisia*, *Eulima* – Philippi, 1844z4: 53, 73, [87], pl. 3, fig. 8. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Syntype, RPMH (Hildesheim). *Acirsa* (*Plesioacirsa*) *leunisia* (Philippi, 1844) (Janssen, 1978a: 68, 1978b: 174–175, pl. 12, fig. 55). *magellanica*, *Scalaria* – Philippi, 1845i: 65. Strait of Magellan, Chile. *Boreoscala magellanica* (Philippi, 1845) (Rios, 1994: 98, pl. 32, fig. 398; Forcelli, 2000: 81, both as *Epitonium*); *Epitonium* (*Nitidiscala*) *magellanicus* (Philippi, 1845), Pliocene to Recent (Valdovinos, 1999: 132; Nielsen & Valdovinos, 2008: 207, fig. 14; Cárdenas et al., 2008: 213–214), or as *Coroniscala magellanica* (Philippi, 1845) (Castellanos, 1990: 21, pl. 2, fig. 17), or as *Cirsotrema magellanica* (Philippi, 1845) (Brown & Neville, 2015: 99). *nodulosa*, *Scalaria* – Philippi, 1887a: 83 [1887b: 78], pl. 9, fig. 18. Lebu or Tubul, Chile; Volckmann; Tertiary. Syntypes, SGO. PI.745 (n = 1, Tubul); SGO.PI.4676 (n = 1, Tubul). *plicosa*, *Scalaria* – Philippi, 1844g: 146, 302, pl. 24, fig. 25 [not “24” as in text]. Lamati Calabria, Italy; fossil. *Punctiscala plicosa* (Philippi, 1844), Late Miocene to Middle Pliocene (Bouchet & Warén, 1986: 548 & fig. 1259; Landau et al., 2006: 55; Brown & Neville, 2015: 29). Type species (OD) of *Punctiscala* de Boury, 1890. *pusilla*, *Scalaria* – Philippi, 1844z4: 54–55, 74, [87], pl. 3, fig. 29. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Syntype, RPMH (Hildesheim), from Freden. *Opalia* (*Pliciscala*) *pusilla* (Philippi, 1844) (Janssen, 1978a: 69–70, 1978b: 175–176, pl. 12, fig. 57; Schnetler & Palm, 2008: 31–32, pl. 3, fig. 7). Type species (OD) of *Funiscala* de Boury, 1891. In establishing *Funiscala*, de Boury (1891: 219–220) designated *S. pusilla* as the type species, but de Boury’s material comprised misidentified specimens of *S. speyeriana*

Sacco, 1891, which must be treated as the type species under ICZN Code Article 70.3 (1999) (Beu, 2011: 18–19; Brown & Neville, 2015: 24–25).

*quadristriata*, *Melania* – Philippi, 1841f: 19; 1844z4: 19, 53 (as *Eulima*), [87], pl. 3, fig. 9. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Acirsa* (*Acirsella*) *quadristriata* (Philippi, 1841) (Janssen, 1978a: 68, 1978b: 175, pl. 12, fig. 56, who dated the species from 1843). Type material lost (R. Janssen, pers. comm., April 2013).

*reticulata*, *Scalaria* – Philippi, 1844z4: 55, [87], pl. 3, fig. 25. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Lectotype, RPMH (Hildesheim), from Freden (designated by Janssen, 1978b: 179–180, pl. 13, fig. 64). *Cirsotrema* (*Cerithiscala*) *reticulatum* (Philippi, 1844) (Janssen, 1978b: 179–180, pl. 13, fig. 64).

*rudis*, *Scalaria* – Philippi, 1841f: 21; 1844z4: 21, [87], pl. 3, fig. 27. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Turriscala* (*Turriscala*) *rudis* (Philippi, 1841) (Janssen, 1978a: 73–74, 1978b: 176–177, pl. 12, fig. 58; Gründel, 1997: 4, pl. 1, fig. 2; Schnetler & Palm, 2008: 32, pl. 3, fig. 8, all of whom dated the species from 1843). Type material lost (R. Janssen, pers. comm., April 2013). Type species (OD) of *Rudiscala* de Boury, 1909.

*trinacria*, *Scalaria* – Philippi, 1844g: 145, 302, pl. 24, fig. 24 [not “23” as in text]. Palermo, Sicily, Italy; fossil.

*volckmanni*, *Scalaria* – Philippi, 1887a: 83 [1887b: 78], pl. 9, fig. 17. Lebu or Tubul, Chile; Volckmann; Tertiary. Holotype, SGO. PI.749.

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“*multistriata*, *Scalaria*” – Philippi, 1844n: 108. This was cited in Sabelli et al. (1990: 181) and Brown & Neville (2015: 109) as if it were a homonym of *Scalaria multistriata* Say, 1826, but it is merely a misuse of Say’s species name.

“*vitrea*, *Scalaria*” – Issel, 1869: 185. Red Sea. Issel credited this manuscript name to Philippi, but did not make it available either.

#### Janthinidae

*incisa*, *Janthina* – Philippi, 1849h: 149. Senegal; Largilliert. “Probably” a synonym of *Janthina exigua* Lamarck, 1816 (Tryon, 1887a: 38).



*patula*, *Janthina* – Philippi, 1844g: 224, 303, pl. 28, fig. 14. Naples. Synonym of *Janthina pallida* W. Thompson, 1840, ex Harvey ms (Priolo, 1959: 186–187 [336–337]; Sabelli et al., 1990: 180).

#### Eulimidae

Eulimidae – Philippi, 1853a: 194. Based on *Eulima* Risso, 1826. Valid family name.

Stylinidae – Philippi, 1853a: 128, 179. Based on *Stylina* Fleming, 1828, *non* Lamarck, 1816. Invalid under ICZN Code Article 39 (1999). Synonym of Eulimidae Philippi, 1853.

*antarctica*, *Eulima* – Philippi, 1887a: 97 [1887b: 91], pl. 11, fig. 15. Navidad, Chile; Tertiary [Miocene].

*minor*, *Niso* – Philippi, 1844z4: 53, 74, [87], pl. 3, fig. 16. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. *Niso* (*Niso*) *minor* Philippi, 1844 (Speyer, 1870a: 72–73, pl. 12, figs. 9–10; Janssen, 1978a: 81–82, 1978b: 188, pl. 13, fig. 78).

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*boscii*, *Melania* – Philippi, 1836a: xi, 157. As “mihi” for a transfer of *Rissoa boscii* Payraudeau, 1826, to *Melania*. *Melanella polita* (Linnaeus, 1758).

*terebellum*, *Niso* – Philippi, 1844g: 136. Tryon (1886a: 353, pl. 77, fig. 17) and Sherborn (1931: 6432) listed this name as of Philippi, but Philippi noted its origin with Chemnitz, from which it was first made available as *Turbo terebellum* Dillwyn, 1817.

#### Triphoridae

*laevum*, *Cerithium* – Philippi, 1845z: 449 [*nomen nudum*]; 1847-l: 63, pl. 9, fig. 11. Magdeburg area, Germany; Tertiary; Sack’s collection. *Ogivia laeva* (Philippi, 1847), Lattdorfian (Oligocene), Germany (Amitrov & Zhegallo, 2007b: 373, 377).

#### Cerithiopsidae

*pygmaeum*, *Cerithium* – Philippi, 1844g: 162–163, 302, pl. 25, fig. 26, 26a. Sicily, Italy. Syntypes, MNHNS 177 (n = 3). Synonym of *Cerithiopsis tubercularis* (Montagu, 1803) (Sabelli et al., 1990: 179).

*pyrgiscus*, *Cerithium* – Philippi, 1887a: 79 [1887b: 74], pl. 8, fig. 17. Lebu, Chile; Tertiary. Possible syntype SGO.PI.760 (but with label by D. Frassinetti, that this specimen is

actually *Terebra costellata* G. B. Sowerby II, 1846); SGO.PI.680 has label “*Cerithium pyrgiscus* (Holotipo)”, but its locality is Navidad, not Lebu. *Cerithiopsis pyrgiscus* (Philippi, 1887) (Cecalupo, 2006: 233).

*trilineatum*, *Cerithium* – Philippi, 1836a: xii, 195, pl. 11, fig. 13; 1844g: 163. Pantelleria Island & Ognina, Catania, Sicily, Italy. Also fossil. Syntype, PHB MB Ga. \_\_\_\_ (XI) (67) (n = 1) (Melitella, Sicily). *Cinctella trilineata* (Philippi, 1836) (Marshall, 1978: 94); *Seila trilineata* (Philippi, 1836) (Priolo, 1958: 131 [300]; Anderson, 1960a: 65–67, pl. 11, figs. 6, 6a; Sabelli, 1990: 179; Cecalupo, 2006: 161); type species (OD) of *Cinctella* Monterosato, 1884. Tembrock (1964b: 330–331, pl. 5, figs. 7–10) determined that some fossil records from northern Europe erroneously attributed to this species were instead referable to *Cerithiella metula* subsp. *zelandica* (Beets, 1946); Janssen (1978a: 64–65, 1978b: 171) determined that Philippi’s own citation of this species from the Oligocene of Germany (1844z4: 56, 75) was instead referable to either *Seila angusta* Tembrock, 1964, or *Cerithiella bitorquatum* (Philippi, 1841) (Newtoniellidae).

#### Newtoniellidae

*bitorquatum*, *Cerithium* – Philippi, 1841f: 23; 1844z4: 23, [87], pl. 4, fig. 5. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Cerithiella* (*Cerithiella*) *bitorquatum* (Philippi, 1841) (Anderson, 1960a: 63, pl. 12, fig. 4; Janssen, 1978b: 171, pl. 12, figs. 48, 49; Rust, 1999: 20–21, both dated the species from 1843). Type material lost (R. Janssen, pers. comm., April 2013).

*pullum*, *Cerithium* – Philippi, 1845i: 66–67. Strait of Magellan, Chile. *Ataxocerithium pulla* (Philippi, 1845) (Carcelles & Williamson, 1951: 275; Castellanos, 1990: 8, pl. 2, figs. 18 & 21; Valdovinos, 1999: 131; Forcelli, 2000: 81; Letelier et al., 2003: 69) or as *Eumetula pulla* (Philippi, 1845) (Reid & Osorio, 2000: 124–125, fig. 70; Cárdenas et al., 2008: 213; Rosenfeld et al., 2015: 71, fig. 5G).

#### Caenogastropoda – *Incertae sedis*

*Dicolpus* – Philippi, 1887a: 40 [1887b: 37], *non* Gerstaecker, 1884 [Insecta]. Type species *Dicolpus obesus* Philippi, 1887 (SD Wenz, 1939: 720). Cossmann (1909: 177) listed this as a junior synonym of *Canthidomus*



Swainson, 1840, itself subsequently synonymized with *Melanopsis* Férussac, 1807 (Pallary, 1916: 76–77). Wenz (1939: 720) initially listed Philippi's genus as questionably within the freshwater Cerithioidea (Thiariidae), and later (1943: 1227) listed Philippi's genus as a possible junior synonym of *Buccinanops* d'Orbigny, 1841 (Nassariidae), but Cernohorsky (1984: 23) made no mention of *Dicolpus* in connection with *Buccinanops* or any other genus of the Nassariidae. The familial placement of this genus and its species remains uncertain, but it is known from Eocene marine outcrops, so that it is probably not referable to "*Melanopsis*" or other freshwater taxa (S. N. Nielsen, in litt., 20 Apr. 2015). If it proves to be a useful taxon, it would have to be renamed because it is a junior homonym.

*anculotoides*, *Dicolpus* – Philippi, 1887a: 41 [1887b: 37], pl. 1, fig. 21. Lebu, Chile; Tertiary. Holotype, SGO.PI.756. *Melanopsis anculotoides* (Philippi, 1887) (Cossmann, 1909: 178). However, being from a marine deposit, unlikely to be a freshwater taxon.

*distortus*, *Dicolpus* – Philippi, 1887a: 41–42 [1887b: 38], pl. 1, fig. 22. Lebu, Chile; Tertiary. Holotype, SGO.PI.755. *Melanopsis distortus* (Philippi, 1887) (Cossmann, 1909: 178). However, being from a marine deposit, unlikely to be a freshwater taxon.

*obesus*, *Dicolpus* – Philippi, 1887a: 40–41 [1887b: 37], pl. 1, fig. 20. Lebu or Tubul, Chile; Tertiary. Syntype, SGO.PI.753 (n = 1, from Tubul). Type species of *Dicolpus* Philippi, 1887. A secondary homonym of *Melanopsis obesa* Bourguignat, 1884; renamed *Melanopsis tumida* Pallary, 1916 (p. 86) (even if no longer classified in that genus, Pallary's replacement name is to be used). As Philippi's species is from a marine deposit, it is unlikely to be a freshwater taxon.

*scalaris*, *Dicolpus* "?" – Philippi, 1887a: 41 [1887b: 38], pl. 1, fig. 24. Lebu, Chile; Tertiary. Holotype, SGO.PI.754. Not mentioned by Cossmann (1909: 178).

*striatus*, *Dicolpus* "?" – Philippi, 1887a: 41 [1887b: 38], pl. 1, fig. 23. Tubul, Chile; Volckmann; Tertiary [early Pleistocene]. *Melanopsis striata* (Philippi, 1887) (Cossmann, 1909: 178). Pallary (1916: 86) stated that Philippi's species was described in the same year as *Melanopsis striata* Handmann, 1887, but the priority of the two names in that year could not be determined, so that he refrained from determining which had to be renamed. How-

ever, as Philippi's species is from a marine deposit, it is unlikely to be a freshwater taxon, so that the two species would not now be placed in the same genus.

#### Buccinidae

*Netrum* – Philippi, 1850j: 118 [24]. Type species (SD Powell, 1966): *Buccinum nifat* Bruguière, 1798. Recent, west Africa. Objective synonym of *Pusionella* Gray, 1847, which has the same type species.

*actonis*, *Buccinum* – Philippi, 1868: 223. Strait of Magellan, Chile [; William Acton]. An indeterminate species (Tryon, 1881: 195).

*adustus*, *Fusus* – Philippi, 1845o: 21 [9], pl. 2, fig. 7. Locality unknown. Synonym of *Penion dilatus* (Quoy & Gaimard, 1833) (Ponder, 1975: 570), itself now regarded as a junior synonym of *Penion sulcatus* (Lamarck, 1816) (Powell, 1979: 200).

*aethiops*, *Buccinum* – Philippi, 1849h: 134; 1849-l: 48–49 [8–9], pl. 1, fig. 15. Locality unknown. Probable synonym of the western Atlantic *Pisania pusio* (Linnaeus, 1758), or *Pisania maculosa* (Lamarck, 1822), from India (Tryon, 1881: 231).

*alternatus*, *Fusus* – Philippi, 1847h: 192 [18], pl. 4, fig. 6; 1860a: 187 [1860b: 168–169]. Locality unknown in original description; in 1860, Philippi reported it from Mejillones, Chile (McLean & Andrade, 1982: 14, erroneously stated that Mejillones was the type locality). Figured syntype, MNHNS 217 (44.0 mm x 23.4 mm); syntype, NHMUK 1923.7.13.10; possible syntypes, SMF 314940 (Chile, ex Philippi) (n = 2) (69.7 mm x 38.6 mm; 58.4 mm x 33.6 mm). Synonym of the Chilean "*Austrofusus*" *fontainei* (d'Orbigny, 1839) (Dall, 1909: 285; McLean & Andrade, 1982: 13–14, figs. 31–39; Nielsen, 2013: 42–44, fig. 4m, n). Beu & Marshall (2010) initially stated that Philippi's species was the type species of *Austrofusus* Kobelt 1879 (by subsequent designation, Cossmann, 1901), but Beu & Marshall (2011) later recognized that Martens (1882) had previously designated *Buccinum nodosum* Gray, 1843, ex Martyn ms, as the type species of *Austrofusus*, so that the "genus for the South American taxa incorrectly referred to *Austrofusus* ... and currently in *Aeneator* Finlay, 1926 remains to be established." Araya (2013) reviewed the Chilean species tentatively attributed to *Aeneator* and noted the potential need for a new genus.



- ambiguus*, *Fusus* – Philippi, 1844i: 107–108 [1–2], pl. 1, fig. 2. Locality unknown. The New Zealand *Zeatrophon ambiguus* (Philippi, 1844) (Radwin & D’Attilio, 1976: 191, pl. 29, figs. 9, 10; Abbott & Dance, 1982: 153), or as *Xymene ambiguus* (Philippi, 1844) (Ponder, 1972: 484–486, figs. 1:3, 2:9, 5:1–5; Powell, 1979: 174, pl. 36, figs. 16, 17). Type species (OD) of *Zeatrophon* Finlay, 1926.
- antarcticus*, *Trophon* – Philippi, 1868: 225. Strait of Magellan, Chile; William Acton. Synonym of *Trophon plicatus* (Lightfoot, 1786) (Forcelli, 2000: 85; Pastorino, 2005a: 60, 63).
- arcticus*, *Fusus* – Philippi, 1850j: 119 [25], pl. 5, fig. 5. Spitzbergen, Arctic Ocean; Kröyer. Synonym of the Arctic *Plicifusus kroeyeri* (Möller, 1842) (Kantor & Sysoev, 2005: 137).
- attenuatus*, *Fusus* – Philippi, 1847-l: 72, pl. 10a, fig. 5. Magdeburg area, Germany; Tertiary; Hallisches Museum. The Lower Oligocene *Exilia attenuata* (Philippi, 1847) (Benson, 1940: 220–221, pl. 1, fig. 1).
- bernardianus*, *Fusus* – Philippi, 1851c: 76. Marquesas; Bernardi. *Pyrula bernardianus* (Philippi, 1851) from French Polynesia (Snyder, 2003: 49).
- borealis*, *Fusus* – Philippi, 1850j: 118–119 [24–25], pl. 5, fig. 2. Spitzbergen, Arctic Ocean; Kröyer. Synonym of the Arctic *Neptunea communis* (Middendorff, 1849) (Snyder, 2003: 53; Kantor & Sysoev, 2005: 134).
- brevicauda*, *Fusus* – Philippi, 1847-l: 71, pl. 10, fig. 15, *non* Deshayes, 1832. Westeregeln; Hallisches Museum; early Oligocene. Renamed *Pseudoneptunea sinodonata* Wrigley, 1953.
- breviculus*, *Fusus* – Philippi, 1845z: 450 [*nomen nudum*], *non* Deshayes, 1834.
- bullatum*, *Buccinum* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 76, pl. 10, figs. 14, 15. Magdeburg area, Germany; Tertiary; Hallisches Museum & Sacks collections. *Pseudocominella bullata* (Philippi, 1847) (Nuttall & Cooper, 1973: 189). Although Nuttall & Cooper (1973) placed this genus and species in the Nassariidae, Cernohorsky (1984: 27) instead suggested that it belongs to the Buccinidae.
- candidissimum*, *Buccinum* – Philippi, 1836a: xiii, 222, pl. 11, fig. 18, 18a; 1844g: 189. Catania, Sicily, Italy. Syntype, ZMB 14941 (9.8 mm x 4.3 mm). *Chauvetia candidissima* (Philippi, 1836) (Sabelli et al., 1990: 194). Senior primary homonym of *B. candidissimum* C. B. Adams, 1845, now treated as *Nassarius candidissimus* (C. B. Adams, 1845), from the Caribbean (e.g., Cernohorsky, 1984: 40), which would require renaming as there are no apparent junior synonyms of the C. B. Adams name (H. H. Kool, in litt., 10 March 2015).
- candidus*, *Fusus* – Philippi, 1849h: 148; 1850j: 117–118 [23–24], pl. 5, fig. 7. Senegal; Largilliert. *Clavatula (Pusionella) candida* (Philippi, 1849) (Nicklès, 1950: 125, fig. 248).
- cecillii*, *Turbinella* “?” – Philippi, 1844z: 166–167. Mouth of the Yang-tse River, China; Largilliert. *Cantharus cecillii* (Philippi, 1844) (Higo et al., 1999: 239; Okutani, 2000: 484–485, fig. 144, as “*C. cecillei*”; Qi, 2004: 93, pl. 57B; Vermeij, 2006: 72, as “*C. cecillei*” and as “1848”).
- chattertoni*, *Buccinum* – Philippi, 1887a: 65 [1887b: 61], pl. 5, fig. 14. Cueva de Cucao, Isla Chiloé, Chile; Enrique Chatterton [Tertiary]. Holotype, SGO.PI.738 (broken).
- chiloensis*, *Buccinum* – Philippi, 1858a: 124–125. Chiloé, Chile. An undetermined species (Tryon, 1881: 195).
- darwinianus*, *Fusus* – Philippi, 1887a: 44–45 [1887b: 41], pl. 2, fig. 7, *nom. nov. pro Fusus regularis* G. B. Sowerby I, 1846, *non* J. Sowerby, 1825. Synonym of *Penion subregularis* (d’Orbigny, 1852), an earlier replacement name (Griffin & Nielsen, 2008: 303, pl. 23, figs. 6, 7), who figured Sowerby’s type material of this species. The material labeled as Philippi’s types in the Museo Nacional, Santiago, Chile (SGO.PI.551, 554, 4533–4535), has no type status, because it was a replacement name.
- decollata*, *Buccinum corniculum* var. – Philippi, 1844g: pl. 27, fig. 11 [name and figure only]. No locality; presumably Sicily. *Amycla corniculum* var. *decollata* (Philippi, 1844) (Bucquoy et al., 1882: 58, pl. 12, fig. 15), or synonym of *Nassa corniculum* (Olivi, 1792) (Priolo, 1965: 109 [611]).
- diminutivum*, *Buccinum* – Philippi, 1887a: 65 [1887b: 61], pl. 5, fig. 12. Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.734 (labeled as “lectotipo”); SGO.PI.4569–4577.
- domeykoanus*, *Fusus* – Philippi, 1887a: 45 [1887b: 42], pl. 2, fig. 10. Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.545 (labeled as “lectotipo”); SGO.PI.4559–4564 (labeled as “paralectotipo”). Either in the *Fusinus* group [Fasciariidae] (Snyder, 2003: 86, 259), or *Fusus (Siphonalia) domeykoanus* Philippi, 1887, Miocene [Buccinidae] (Tavera, 1979: 86–87, pl. 17, fig. 46).



- dumale*, *Buccinum* – Philippi, 1851b: 60. Marquesas; Bernardi. Syntype, ZMB 117926 (n = 1) (20.9 mm x 9.4 mm). *Phos dumale* (Philippi, 1851) (Tryon, 1881: 220).
- elegantulus*, *Fusus* – Philippi, 1844z4: 59, 76, [87], pl. 4, fig. 16. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Type material in PHB MB Ga. 71 (Tembrock, 1968: 217, as “holotypus”). *Scalaspira (Scalaspira) elegantula* (Philippi, 1844) (Tembrock, 1965a: 434–435, pl. 5, fig. 12; 1968: 216–218, pls. 1, figs. 2–5, pl. 3, figs. 2–7, pl. 5, figs. 6–7, pl. 6, fig. 7, pl. 7, fig. 11; Janssen, 1978a: 102, 1979a: 286–287, pl. 15, fig. 7; Amitrov & Zhegallo, 2007a: 26).
- exile*, *Buccinum* – Philippi, 1844g: 192–193, pl. 27, fig. 16, 16a, *non* Gmelin, 1791. Palermo, Sicily, Italy; fossil.
- glabriculus*, *Fusus* – Philippi, in Volger, 1845: 34, 36; 1847-l: 73, pl. 10, fig. 7. Lüneburg, Lower Saxony, Germany [Middle] Miocene. *Scalaspira glabricula* (Philippi, in Volger, 1845) (Tembrock, 1965a: 436, 1968: 255, pl. 4, figs. 8–9). Type material lost (R. Janssen, pers. comm., April 2013).
- gracile*, *Buccinum* – Philippi, 1887a: 65 [1887b: 61], pl. 6, fig. 10, *non* da Costa, 1778, *non* Reeve, 1846, *non* S. V. Wood, 1848. Navidad, Chile; Tertiary [Miocene]. Griffin & Hünicken (1994: 266) stated that this species potentially “could be included” in *Pseudofax* Finlay & Marwick, 1937 (Buccinidae), but as it is a homonym, it would require renaming.
- granulatum*, *Buccinum* – Philippi, 1836a: xiii, 226, pl. 11 [not pl. 12, as in text], fig. 22, *non* Born, 1778, *non* J. Sowerby, 1815; 1844g: 191. Militello, Sicily; fossil. Syntype, PHB MB Ga. 448 (n = 1) (7.8 mm x 4.9 mm).
- gregarius*, *Fusus* – Philippi, in Volger, 1845: 34, 36–37; 1847-l: 73, pl. 10, fig. 8. Lüneburg, Lower Saxony, Germany [Middle] Miocene. *Scalaspira gregaria* (Philippi, 1845) (Tembrock, 1968: 258–261, pl. 13, fig. 9, pl. 14, figs. 10–13, pl. 15, figs. 2–6); *Colus gregarius* (Philippi, in Volger, 1845) (R. Janssen, pers. comm., April 2013). Type material lost (R. Janssen, pers. comm., April 2013). Type species (SD Wenz, 1943) of *Eurydike* Kautsky, 1925.
- guttatum*, *Buccinum* – Philippi, 1841b: 266. Java “?”. Possibly a senior synonym of *Pisania cingulata* (Reeve, 1847) (Tryon, 1881: 250).
- hoffmanni*, *Pleurotoma* “?” – Philippi, 1845z: 449 [*nomen nudum*]; 1847-l: 65–66, pl. 9, fig. 5. Magdeburg area, Germany; Tertiary; Sack’s & Halleschen Museum collections. *Scalaspira (S.) hoffmanni* (Philippi, 1846), Oligocene of Germany (Tembrock, 1964a: 309, pl. 2, figs. 4a–b).
- hupeanum*, *Buccinum* – Philippi, 1887a: 64 [1887b: 60], pl. 6, fig. 7. Hualpen, Chile. Syntype, SGO.PI.735 (n = 1). Synonym of *Fusus difficilis* d’Orbigny, 1835 (Wilckens, 1904: 210–213, pl. 18, fig. 6), although Feruglio (1937: 156) suggested that this species may actually be a *Phasianella* (Phasianellidae).
- hupeanus*, *Fusus* – Philippi, 1887a: 51 [1887b: 48], pl. 2, fig. 18, *nom. nov. pro Fusus clathratus* Hupé, 1854, *non* “Deshayes” (but actually *non* J. De C. Sowerby, 1836, and *non* Dujardin, 1837); 1897: pl. 3, fig. 2. Synonym of “*Aeneator*” *cleryanus* (d’Orbigny, 1841) (Griffin & Nielsen, 2008: 293–295, pl. 20, figs. 5–9), who figured the type material of both Hupe’s and d’Orbigny’s species.
- janeirensis*, *Buccinum* – Philippi, 1849h: 133–134; 1849-l: 49 [9], pl. 1, fig. 16. Rio de Janeiro, Brazil; Kröyer. Synonym of the western Atlantic *Pisania pusio* (Linnaeus, 1758) (Rios, 1994: 121, pl. 39, fig. 511).
- laevis*, *Fusus* – Philippi, 1887a: 262 [1887b: 252], pl. 3, figs. 3, 24 [name and figure, no description], *non* Mörch, 1869. Presumably Chile; Tertiary. Syntype, SGO.PI.772 (n = 1, from Lebu, labeled as “lectotipo”).
- lautari*, *Fusus* – Philippi, 1887a: 49–50 [1887b: 46], pl. 3, fig. 12. Lebu, Chile; Volckmann; Tertiary.
- leucozonum*, *Buccinum* – Philippi, 1844n: 111–112. Palermo, Sicily, & Rhodum, Mediterranean. The type species (M) of *Enginella* Monterosato, 1917, is *Murex bicolor* Cantraine, 1835, *non* Risso, 1826, *non* Valenciennes, 1832, and Philippi’s *B. leucozonum* is the next available name for this species (Cernohorsky, 1975b: 200, who treated *Enginella* as a subgenus of *Cantharus*). *Engina leucozona* (Philippi, 1844) (Sabelli et al., 1990: 195, 399, Bouchet et al., 2001: 193, and Brunetti & Della Bella, 2014: 12, 28, fig. 11-F, all as “1843”).
- limbatus*, *Fusus* – Philippi, 1844i: 111 [5], pl. 1, fig. 9. West Indies. Philippi speculated that it might be a juvenile of *Buccinum dorbignyi* Payraudeau, 1826, which would make it a synonym of the Mediterranean *Polia dorbignyi* (Payraudeau, 1826) (Snyder, 2003: 129, 268).
- luneburgensis*, *Fusus* – Philippi, in Volger, 1845: 34, 36; 1847-l: 74, pl. 10a, fig. 6.



- Lüneburg, Lower Saxony, Germany; [Middle] Miocene. *Scalaspira luneburgensis* (Philippi, in Volger, 1845) (Tembrock, 1968: 244–246, pl. 9, figs. 6–7). Type material lost (R. Janssen, pers. comm., April 2013).
- lupinus*, *Fusus* – Philippi, 1850j: 118 [24]. Locality unknown. *Pusionella lupinus* (Philippi, 1850) (Tryon, 1881: 257).
- luridum*, *Buccinum* – Philippi, 1849h: 137; 1849-l: 46 [6], pl. 1, fig. 10. New Zealand; Largilliert. Synonym of *Cominella (Josepha) glandiformis* (Reeve, 1847) (Powell, 1979: 193, pl. 40, fig. 14).
- macsporrani*, *Fusus* – Philippi, 1887a: 45 [1887b: 42], pl. 2, fig. 9, as “*F. MacSporran*”; 1897: pl. 3, fig. 6, 6a, 6b, as “*F. maesporran*”. Lebu, Chile; MacSporran; Tertiary. Holotype, SGO.PI.557. *Penion macsporrani* (Philippi, 1887); Miocene (Frassinetti, 2006: 67, figs. 10, 11).
- magellanicum*, *Buccinum* – Philippi, 1849h: 138; 1849-l: 48 [8], pl. 1, fig. 14. Strait of Magellan, Chile; E. B. Philippi. *Pareuthria magellanica* (Philippi, 1849) (Carcelles & Williamson, 1951: 296; Powell, 1951: 133; Valdovinos, 1999: 139; Letelier et al., 2003: 83).
- microstomus*, *Fusus* – Philippi, 1845z: 450 [*nomen nudum*].
- minimum*, *Buccinum* – Philippi, 1836a: xiii, 222, *non* Berkenhout, 1795, *non* Turton, 1802. Palermo & Catania, Sicily, Italy. Syntypes, SMF 314961 (n = 3) (Sicily). Synonym of *Chauvetia brunnea* (Donovan, 1804) (Sabelli et al., 1990: 194).
- moestum*, *Buccinum* – Philippi, 1851b: 60–61. Locality unknown. Possible syntypes, SMF 314779 (10.9 mm x 6.2 mm; 10.5 mm x 6.5 mm). *Pisania moestum* (Philippi, 1851) (Tryon, 1881: 146).
- multangulus*, *Fusus* – Philippi, 1848c: 25–26; 1850j: 117 [23], pl. 5, fig. 6. Yucatan, Mexico; Largilliert. Syntypes, Muséum de Rouen 166901043 (n = 7) (largest, 26.7 mm x 15.6 mm); MNHN Paris 6448 (n = 2). *Cantharus multangulus* (Philippi, 1848) (Robertson, 1957), or as *Hesperisternia multangula* (Philippi, 1848) (Vermeij, 2006: 81; Tunnell et al., 2010: 215).
- oncodes*, *Fusus* – Philippi, 1887a: 45–46 [1887b: 42], pl. 2, fig. 11. Navidad, Chile; Tertiary. Holotype, SGO.PI.579. *Fusus (Siphonalia) oncodes* Philippi, 1887, Miocene (Tavera, 1979: 87, pl. 17, figs. 47–49), or as *Penion oncodes* (Philippi, 1887), Miocene (Frassinetti, 2006: 67).
- patagonicum*, *Buccinum* – Philippi, 1845i: 68–69; 1849-l: 46–47 [6–7], pl. 1, fig. 11. Strait of Magellan, Chile. Perhaps synonym of *Pareuthria plumbea* (Philippi, 1844) (Tryon, 1881: 150, 263; Letelier et al., 2003: 83).
- plumbeus*, *Fusus* – Philippi, 1844i: 108 [2], pl. 1, fig. 3. Chile; E. B. Philippi. Possible syntypes, ZMB 11515 (n = 4) (“Magellan str. Philippi”); ZMB 112886 (n = 2). *Atractodon plumbeus* (Philippi, 1844) (Dall, 1909: 213); *Pareuthria plumbea* (Philippi, 1844) (Carcelles & Williamson, 1951: 295; Castellanos, 1992a: 13–14, pl. 3, fig. 37; Gordillo et al., 1992: 46; Valdovinos, 1999: 139; Snyder, 2003: 163; Aguirre et al., 2009: 428, 430, pl. 6, fig. 28), or a junior synonym of *Pareuthria fuscata* (Bruguière, 1789) (Reid & Osorio, 2000: 126–127, fig. 4C). Type species (SD Tomlin, 1932) of *Pareuthria* Strebel, 1905.
- pusillum*, *Buccinum* – Philippi, 1844g: 192, 303, pl. 27, fig. 15 [in text in error as 14], *non* Pfeiffer, 1840. Palermo, Sicily, & Castell’Arquato, Italy; fossil. Syntypes, SMF 314577 (n = 2) (12.3 mm x 6.8 mm; 11.1 mm x 4.6 mm).
- pusillum*, *Buccinum* – Philippi, 1851b: 62, *non* Philippi, 1844. Locality unknown. Tryon (1881: 266) listed this name in his Index, with no status given.
- retusum*, *Gastrium* – Philippi, 1887a: 63 [1887b: 59], pl. 6, fig. 3. Algarrobo, Chile; Cretaceous. Holotype, SGO.PI.765 (Nielsen & Frassinetti, 2003: 91, figs. 13, 14). *Sulcobuccinum retusum* (Philippi, 1887) (Vermeij, 1998: 82); previously classified in *Buccinorbis* Conrad, 1865 (e.g., Vermeij & DeVries, 1997: 27–28), now regarded as a junior synonym of *Sulcobuccinum* d’Orbigny, 1850.
- ruralis*, *Fusus* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 72, pl. 10, fig. 10. Magdeburg area, Germany; Tertiary; Hallisches Museum; fossil. *Scalaspira (Kautskyella) ruralis* (Philippi, 1847) (Tembrock, 1964a: 308–309), or synonym of *Scalaspira (Vagantospira) multisulcatus* (Nyst, 1845), Oligocene (Gründel, 1991: 102, pls. 1, figs. 5–6, 10).
- scabriculus*, *Fusus* – Philippi, 1847-l: 74, pl. 10a, fig. 4. Walle, Niedersachsen, Germany; Oligocene (Rupelian). *Metula (Daphnobela) scabricula* (Philippi, 1847) (Janssen, 1979a: 294, pl. 16, fig. 20).
- scacchianum*, *Buccinum* – Philippi, 1844g: 188–189, 303, pl. 27, fig. 5, 5a. Naples, Taranto & Palermo, Sicily, Italy. *Polia scacchiana* (Philippi, 1844) (Sabelli et al., 1990: 196), or *Aplus scacchianus* (Philippi, 1844), Pliocene (Brunetti & Della Bella, 2014: 12,



fig. 10-D), or synonym of either *Pisania picta* (Scacchi, 1836) (Priolo, 1965: 92–93 [594–595] or of *Anna massena* Risso, 1826 (Vermeij, 2006: 72).

*solitarius*, *Fusus* – Philippi, in Volger, 1845: 34, 37; 1847-l: 73, pl. 10, fig. 9. Lüneburg, Lower Saxony, Germany, [Middle] Miocene. *Scalaspira solitaria* (Philippi, 1845) (Tembrock, 1968: 261); *Colus solitarius* (Philippi, in Volger, 1845) (R. Janssen, pers. comm., April 2013). Type material lost (R. Janssen, pers. comm., April 2013).

*spinulosum*, *Buccinum* – Philippi, 1844g: 191–192, 303, pl. 27, fig. 13. Monterosso, Lamo & Stilo, Calabria, Italy; fossil.

*striatum*, *Buccinum* – Philippi, 1844g: 193, 303, as “Sow.”, pl. 27, fig. 1, *non* Pennant, 1777. Palermo, Sicily, & Carrubbare, Rhegium, Calabria, Italy; fossil. Synonym of *Buccinum humphreysianum* Bennet, 1824 (Priolo, 1965: 93–95 [595–597]; Bouchet & Warén, 1985: 188–189, figs. 468, 494–496; Sabelli et al., 1990: 193).

*subcoronatum*, *Buccinum* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 77, pl. 10, fig. 17. Magdeburg area, Germany; Tertiary; Sack’s collection & Hallisches Museum. Koenen (1889: 237–241, pl. 21, figs. 1–3) concluded that this was a junior synonym of “*Buccinum (Cominella) bullatum*” Philippi, 1847, *supra*, which may now be referable to the Nassariidae (Nuttall & Cooper, 1973), or to the Buccinidae (Cernohorsky, 1984: 27).

*villanus*, *Fusus* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 72–73, pl. 10, fig. 6. Magdeburg area, Germany; Tertiary; Hallisches Museum. Synonym of *Scalaspira (Vagantospira) multisulcatus* (Nyst, 1845), Oligocene (Tembrock, 1964a: 305–307, pl. 1, figs. 3–4, pl. 3, fig. 4; Tembrock, 1968: 263–264, pl. 16, figs. 2–3; Gründel, 1991: 102, pls. 1, figs. 5–6, 10); *Scalaspira (Vagantospira) villana* (Philippi, 1847) (Amitrov & Zhegallo, 2007a: 21), or as *Vagantospira villana* (Philippi, 1847) (R. Janssen, pers. comm., April 2013).

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“*chilensis*, *Fusus*” – Bandel & Stinnesbeck (2000: 767) attributed this species to “Philippi, 1887”, but Philippi (1887: 42, pl. 3, figs. 3, 24) correctly cited this species as *Fusus chilinus* d’Orbigny, 1847.

“*extensum*, *Buccinum*” – Philippi, 1849u: 70 [18], pl. 2, fig. 11. This species was listed by Sherborn (1926: 2284) as a Philippi name, but the header and signature on the de-

scription indicate that it should be credited to Dunker. (Philippi did add a note after its description.) *Cantharus extensum* (Dunker in Philippi, 1849) (Tryon, 1881: 156, 256).

#### Columbellidae

*acute-costatum*, *Buccinum* – Philippi, 1844g: 192, 303, pl. 27, fig. 14, as “*acute-costatum*”. Stillo & Monasterace, Calabria, Italy; fossil. In Sherborn (1922: 60) as *B. acuto-costatum*. *Amphissa acute-costata* (Philippi, 1844) (Bouchet & Warén, 1985: 165–167, figs. 392, 395–398; Sabelli et al., 1990: 205, as *A. “acuto-costata”*; Sysoev, 2014: 143); incorrectly listed as a junior synonym of *Amphissa haliaeeti* (Jeffreys, 1867) by Fretter & Graham (1985: 462–463, fig. 321).

*antarcticum*, *Buccinum* – Philippi, 1868: 222. Strait of Magellan, Chile; William Acton. Tryon (1881: 195) listed this as “? *Columbella*” in his treatment of the Buccinidae, but did not mention it in his treatment of the Columbellidae (Tryon, 1882b–1883a). Pace (1902: 54) listed this species in the Columbellidae.

*avena*, *Buccinum* – Philippi, 1846h: 52–53. Chile. Tryon (1881: 235) listed this as “*Columbella*” in his treatment of the Buccinidae, but did not mention it in his treatment of the Columbellidae (Tryon, 1882b–1883a). Pace (1902: 58) listed this species in the Columbellidae, and it is a potential secondary senior homonym of *Columbella avena* Reeve, 1859, from South Africa, placed in *Mitrella* by some websites. However, Kilburn & Marais (2010: 63) stated that Reeve’s species does not match any known South African species.

*coccinea*, *Buccinum linnaei* – Philippi, 1836a: 225, as “*var. γ [gamma] coccinea*”. Sicily, Italy. However, Philippi (1844: 190) subsequently synonymized *B. linnaei* with *B. corniculatum* Lamarck, 1822, itself a junior synonym of *Mitrella scripta* (Linnaeus, 1758), and made no mention of the “varieties” from 1836. Hence, “*coccinea*” was never made available pursuant to ICZN Code Article 45.6.4.1 (1999). Sabelli et al. (1990: 206) listed this as *Mitrella coccinea* (Philippi, 1836), but Philippi’s name is unavailable.

*cosentini*, *Terebra* – Philippi, 1836a: xiii, 227–228, footnote, pl. 12, fig. 29. “Naples”. The western Atlantic *Mazatlanian cosentini* (Philippi, 1836) (Bouchet & Gofas, 1983), described with an erroneous locality. Type species (SD Wenz, 1941) of *Mazatlanian* Dall, 1900, a new name for *Euryta* H. Adams & A.



- Adams, 1858, *non* Gistel, 1848. Lectotype, ZMB 11481 ("Neapel") (12.8 mm x 4.7 mm), designated by Monsecour & Köhler (2006: 288, fig. 14). *Mazatlanian hesperia* Pilsbry & Lowe, 1932, is now considered to be a separable eastern Pacific cognate (McLean, 1998).
- ebenum*, *Columbella* – Philippi, 1868: 223; 1887a: 66 [1887b: 62, as "*C. benum*"], unfigured. Coast at Isla Blanca, Algarrobo, Chile; Quaternary. SGO.PI.757 is labeled as the "holotipo", but it was not collected until 1878, after the original description. Synonym of *Columbella (Alia) unifasciata* (G. B. Sowerby I, 1832) (Tryon, 1883a: 117).
- elongata*, *Columbella rustica* – Philippi, 1836a: 228, pl. 12, fig. 11 [not cited in text]. Palermo, Sicily, Italy. Lectotype, ZMB 13994 (Palermo) (22.1 mm x 10.5 mm), designated by Monsecour & Köhler (2006: 289, fig. 18); paralectotypes, ZMB 112717 (n = 2) (Palermo); SMF 313169 (n = 2) (24.6 mm x 11.1 mm; 22.9 mm x 10.9 mm). Synonym of *Columbella rustica* (Linnaeus, 1758) (Bucquoy et al., 1882: 72, pl. 12, figs. 32–33).
- exilis*, *Columbella* – Philippi, 1849r: 23. Red Sea; Th. Philippi. Lectotype, ZMB 109705a ("Aden"), designated by Monsecour & Köhler (2006: 289, fig. 20); paralectotypes, ZMB 109705b (n = 2). *Zafra exilis* (Philippi, 1849). Segers & Swinnen (2003) determined that this species, native to the Red Sea, was accidentally introduced into the Canary Islands.
- exilis*, *Columbella* – Philippi, 1887a: 66 [1887b: 62], pl. 6, fig. 9, *non* Philippi, 1849r. Navidad, Chile; Tertiary [Miocene].
- fulgurata*, *Terebra* – Philippi, 1846h: 53. Mazatlán, Sinaloa, Mexico. The eastern Pacific and western Atlantic *Mazatlanian fulgurata* (Philippi, 1846) (Keen, 1971: 588–589, fig. 1226; Radwin, 1978: 337, fig. 25; Ramírez et al., 2003: 262). Type material not located in NHMUK (McLean, 1998).
- hordacea*, *Columbella* – Philippi, 1849r: 23–24. Red Sea; Th. Philippi. *Columbella (Seminella) hordacea* (Philippi, 1849) (Tryon, 1883a: 179).
- pallida*, *Columbella* – Philippi, 1846h: 53–54, *non* Deshayes, 1844. Mazatlán, Sinaloa, Mexico. Tryon (1883a: 111) stated that "This species ... remains unrecognized".
- secalinum*, *Buccinum* – Philippi, 1846h: 53. Chile. Lectotype, ZMB 112715a ("Chili"), designated by Monsecour & Köhler (2006: 300, fig. 54); paralectotypes, ZMB 112715b (n = 3). *Cilara secalina* (Philippi, 1846), Chile (Marincovich, 1973: 35, fig. 76; Valdovinos, 1999: 137; Letelier et al., 2003: 81; Ramírez et al., 2003: 262); type species (M) of *Cilara* Thiele, 1924.
- spadicea*, *Columbella* – Philippi, 1846h: 54. Mazatlán, Sinaloa, Mexico. Lectotype, ZMB 112738 ("Mazatlan") (9.1 mm x 3.9 mm), designated by Monsecour & Köhler (2006: 301, fig. 58); paralectotypes, ZMB 112738b (n = 1); NHMUK 20100334 (n = 4) (figured by Keen, 1971: 581, fig. 1192). *Anachis (Costanachis) spadicea* (Philippi, 1846) (Keen, 1971: 580–581, fig. 1192). Listed by Ruhoff (1980: 501) as being by "Philippi, in Reeve, 1858".
- taeniata*, *Columbella* – Philippi, 1846h: 54–55, *non* Link, 1807. Mazatlán, Sinaloa, Mexico. Synonym of *Anachis (Parvanachis) gaskoini* Carpenter, 1857 (Keen, 1971: 584).

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"*mitrula*, *Buccinum*" – Philippi, 1849u: 69–70, pl. 2, fig. 9. This species was listed by Sherborn (1928: 4112) as a Philippi name, but the header and signature on the description indicate that it should be credited to Dunker. (Philippi did sign a note after its description.) Monsecour & Köhler (2006: 295) correctly attributed this species to Dunker, in Philippi, 1849. However, it is *non* J. Sowerby, 1822.

#### Fasciolaridae

- albus*, *Fusus* – Philippi, 1851c: 75–76, *non* McAndrew & Forbes, 1847. Locality unknown; Bernardi. Possible synonym of the Japanese *Fusinus spectrum* (A. Adams & Reeve, 1850) (Snyder, 2003: 36–37, 282).
- alfonsoi*, *Fusus* – Philippi, 1887a: 52 [1887b: 48], pl. 2, fig. 4. Coquimbo, Chile; Quaternary. Holotype, SGO.PI.548. *Fusinus* group (Snyder, 2003: 37, 248).
- cheruscus*, *Fusus* – Philippi, 1844z4: 59, [87], pl. 4, fig. 21. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. *Streptochetus cheruscus* (Philippi, 1844) (Tembrock, 1965b: 432–433, pl. 34, figs. 7–8; Janssen, 1978a: 111–112, 1979a: 297–298, pl. 16, fig. 25; Rust, 1999: 25; Snyder, 2003: 64). Lectotype, PHB MB Ga. 123 (T) 96 (27.6 mm x 11.5 mm) (Freden, near Alfeld/Leine, Germany; Late Oligocene), designated by Cadée & Janssen (1994: 43, pl. 1, fig. 9), who noted that of the two syntypes, only the figured specimen, collected by Leunis, was extant; they stated that the specimen collect-



- ed by Römer was no longer extant. However, there also exists PHB MB Ga. 7466 (T) (96), labeled as paralectotypes ( $n = 3$ ). Tembrock (1965b: 432) stated that PHB MB Ga. 123 was the "Holotypus (kraft Monotypie)" but there were multiple syntypes so her statement was not a lectotype designation.
- chonoticus*, *Fusus* – Philippi, 1858b: 23. Islas Chonos, Chile; Fr. Fonk. *Fusinus chonoticus* (Philippi, 1858) (Snyder, 2003: 65, 254).
- closter*, *Fusus* – Philippi, 1850j: 115–116 [21–22], pl. 5, fig. 1. Margarita Island, West Indies [Venezuela]; Gruner coll. Synonym of the Caribbean *Fusinus ansatus* (Gmelin, 1791) (Snyder, 2003: 67).
- crassus*, *Fusus* – Philippi, 1887a: 48 [1887b: 44–45], pl. 3, fig. 6, *non* T. Brown, 1827. Matanzas, Chile. Holotype, SGO.PI.553. *Fusinus* group (Snyder, 2003: 75, 256), or junior synonym of *Cominella obesus* (Philippi, 1887) (Steinmann & Wilckens, 1908: 60–64, pl. 6, figs. 3–5).
- crocata*, *Fasciolaria* – Philippi, 1848c: 25; 1849w: 74–75 [2–3], pl. 1, fig. 3. Yucatan, Mexico; Largilliert. Syntypes, Muséum de Rouen 1670010019 ( $n = 2$ ) (186.7 mm x 36.7 mm; 65.2 mm x 25.9 mm). Probably mislocalized and a synonym of the Panamic *Pleuroploca princeps* (G. B. Sowerby I, 1825) (Snyder, 2003: 78).
- cygneus*, *Fusus* – Philippi, 1851c: 76. Locality unknown; Bernardi. *Fusinus cygneus* (Philippi, 1851) (Snyder, 2003: 79, 257).
- exaratus*, *Fusus* – Philippi, 1887a: 46 [1887b: 43], pl. 2, fig. 14, *non* Beyrich, 1856. Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.550 (labeled as "lectotipo"); SGO.PI.4536 ( $n = 1$ , labeled as "paralectotipo"). *Fusinus* group (Snyder, 2003: 92, 260).
- foncki*, *Fusus* – Philippi, 1887a: 49 [1887b: 45], pl. 3, fig. 8. Lebu, Chile; W. Fonck; Tertiary. Syntype, SGO.PI.569 (labeled as "lectotipo"); SGO.PI.4539 (labeled as "paralectotipo"). *Fusinus* group (Snyder, 2003: 97, 261).
- fusiformis*, *Fasciolaria* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 70, pl. 10, fig. 1. Specimen lacking siphonal canal: Nase; Sacks collection & Welsleben; Oberbergamtes collection; Tertiary.
- gilvus*, *Fusus* – Philippi, 1849h: 148. China; Largilliert. *Fusinus gilvus* (Philippi, 1849) (Snyder, 2003: 103, 263).
- guttatus*, *Fusus* – Philippi, 1844i: 109–110 [3–4], pl. 1, fig. 6, ex Busch ms. Locality unknown. The description was signed by Philippi and so he has to take credit for the name. *Fusinus* group (Snyder, 2003: 107, 264, as "Busch, in Philippi").
- heterocyclus*, *Fusus* – Philippi, 1887a: 43 [1887b: 40], pl. 3, fig. 9. Algarrobo, Chile; Landbeck; Cretaceous. Syntypes, SGO.PI.570 (labeled as "lectotipo"); SGO.PI.4529 ( $n = 1$ , labeled as "paralectotipo"). *Fusinus* group (Snyder, 2003: 138, 265).
- ischnos*, *Fusus* – Philippi, 1887a: 49 [1887b: 46], pl. 3, fig. 11. Lebu; Tertiary. Holotype, SGO.PI.585. *Fusinus* group (Snyder, 2003: 118, 266).
- lebuensis*, *Fusus* – Philippi, 1887a: 50 [1887b: 47], pl. 3, fig. 14. Lebu, Chile; Tertiary. Syntypes, SGO.PI.549 (labeled as "lectotipo"); SGO.PI.4541–4547 (labeled as "paralectotipo"). *Fusinus* group (Snyder, 2003: 126, 268).
- liratus*, *Fusus* – Philippi, 1887a: 49 [1887b: 46], pl. 3, fig. 10, *non* Gould, 1848, *non* Pease, 1868. Lebu, Chile; Tertiary. Syntypes, SGO.PI.597 (labeled as "lectotipo"); SGO.PI.4540 ( $n = 1$ , labeled as "paralectotipo"). *Fusinus* group (Snyder, 2003: 130, 269).
- marmoratus*, *Fusus* – Philippi, 1846p: 120 [14], pl. 3, fig. 7. Locality unknown. Issel (1869: 138, 272) recorded this species from the Red Sea and Australia, but now treated as the Brazilian *Fusinus marmoratus* (Philippi, 1846) (Rios, 1994: 132, pl. 42, fig. 569); listed as an European species by Bouchet et al. (2001: 192).
- metzdorfi*, *Fusus* – Philippi, 1887a: 43 [1887b: 39–40], pl. 3, fig. 1. Isla Quiriquina, Chile; Paul Metzdorf. Holotype, SGO.PI.568. *Fusinus* group (Snyder, 2003: 111, 270).
- minor*, *Fusus obesus* – Philippi, 1887a: 47–48 [1887b: 44], *non* Link, 1807, and nine other earlier uses of this name. Matanzas & Cueva de Cucao, Chile. Syntypes, SGO.PI.594 ( $n = 1$ ), SGO.PI.582 ( $n = 1$ ). *Fusinus* group (Snyder, 2003: 151, 273). Synonym of *Cominella cossmanni* (Ihering, 1907), from Santa Cruz, Lower Miocene (Parodiz, 1996: 215).
- modestus*, *Fusus* – Philippi, 1844i: 111 [5], pl. 1, fig. 11, ex Anton ms [*non* Philippi, 1887a, b]. Locality unknown. Possibly an eastern Pacific *Latirus* (Snyder, 2003: 141, 205). *Fusus modestus* Gould, 1860, is now *Lirabuccinum fuscolabiatum* (E. A. Smith, 1875).
- modestus*, *Fusus* – Philippi, 1887a: 50 [1887b: 46–47], pl. 3, fig. 13a, *non* Philippi, 1844, *non* Gould, 1860. Lebu, Chile; Tertiary. Holotype, SGO.PI.578. Synonym of *Austrotoma echinulata* (Hupé, 1854) (Oligocene-Miocene) (Beu, 2011: 99).



- nigrinus*, *Fusus* – Philippi, 1858b: 23. Islas Chonos, Chile; Fr. Fonk. *Fusinus nigrinus* (Philippi, 1858) (Snyder, 2003: 148, 273).
- nodulifer*, *Fusus* – Philippi, 1887a: 48 [1887b: 45], pl. 3, fig. 7. Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.546 (labeled as "lectotipo"); SGO.PI.5438 (n = 1, labeled as "paralectotipo"). *Fusinus* group (Snyder, 2003: 150, 273).
- obesus*, *Fusus* – Philippi, 1887a: 47–48 [1887b: 44], pl. 3, fig. 4 [labeled "4b" on pl.], non Michelotti, 1847, non Schafhäutl, 1863, non G. B. Sowerby II, 1889. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.586. *Fusinus* group (Snyder, 2003: 151, 273), *Cominella obesus* (Philippi, 1887) (Steinmann & Wilckens, 1908: 60–64, pl. 6, figs. 3–5).
- obscurus*, *Fusus* – Philippi, 1844i: 108 [2], pl. 1, fig. 5. Locality unknown. Tryon (1881: 67, pl. 40, fig. 176) listed this among the "Doubtful and spurious Fusidae". *Fusinus* group (Snyder, 2003: 153, 273).
- ovallei*, *Fusus* – Philippi, 1887a: 51 [1887b: 47], pl. 3, fig. 18. Tubul, Chile; Volckmann, Puchoco & Navidad; Tertiary. Syntypes, SGO.PI.593 (n = 1, Navidad); SGO.PI.4548–4552 (Lebu [Tubul]). *Fusinus* group (Snyder, 2003: 154, 274).
- oxytropis*, *Fusus* – Philippi, 1887a: 50 [1887b: 47], pl. 3, fig. 15. Tubul, Chile; Volckmann & Navidad; Tertiary. Syntype, SGO.PI.563 (labeled as "holotipo" but the species is known from two localities). Olivera et al. (1994: 285, fig. 5.6) illustrated this syntype, and concluded that this species "might be assigned to *Fulgurofusus* Grabau, 1904" (Columbariinae). *Fusinus* group (Snyder, 2003: 154, 274).
- pfeifferi*, *Fusus* – Philippi, 1846p: 117 [11], pl. 3, fig. 1. Locality unknown; Pfeiffer coll. Possibly *Pseudolatirus* from the Philippine Islands (MacNeil, 1961: 83).
- polypleurus*, *Fusus* – Philippi, 1887a: 48 [1887b: 44], pl. 3, fig. 5. Navidad & Matanzas, Chile; Tertiary. Syntypes, SGO.PI.591 (labeled as "lectotipo"); SGO.PI.4537 (n = 1, labeled as "paralectotipo"). *Fusinus* group (Snyder, 2003: 164, 276), or a junior synonym of *Cominella obesus* (Philippi, 1887) (Steinmann & Wilckens, 1908: 60–64, pl. 6, figs. 3–5).
- pulchellus*, *Fusus* – Philippi, 1840a: 68; 1844g: 178, 179, 302, pl. 25, fig. 28. Sicily, Italy. ZMB 82337 is labeled as a type, but it is Monterosato's specimen, from Sardinia. Renamed *Murex philippii* by Monterosato (1872a: 32, 43; 1872b: 47), who placed Philippi's species in *Murex*, in which it became a transient junior secondary homonym of *Murex pulchellus* Lamarck, 1822. *Fusinus pulchellus* Philippi, 1840 (Sabelli et al., 1990: 197; Giribet & Peñas, 1997: 51 [13], both as "1844"). Also unnecessarily renamed as *Fusinus quandumpulchellus* Snyder, 2000.
- pusio*, *Fusus* – Philippi, 1887a: 50 [1887b: 46], pl. 3, fig. 13. Navidad, Chile; Tertiary [Miocene]. *Fusinus* group (Snyder, 2003: 169, 277).
- reeveanus*, *Fusus* – Philippi, 1850j: 119 [25]. This was named for *Fusus multicarinatus* Lamarck, 1822, *sensu* Reeve (1847: pl. 6, fig. 22), non Lamarck, 1822. Locality unknown. Probable syntype, NHMUK 20110267 (100.4 mm x 30.0 mm) matches Reeve's figure. The western Pacific *Fusinus reeveanus* (Philippi, 1850) (Higo et al., 1999: 262).
- reevei*, *Fasciolaria* – Philippi, 1850k: 121 [7], pl. 3, fig. 2, ex Jonas ms. Locality unknown. This species was indicated as being "in litteris", with Jonas mentioned in the third person in the discussion. Synonym of the western Atlantic *Pleuroploca gigantea* (Kiener, 1840), or of the Panamic *P. princeps* (G. B. Sowerby I, 1825) (Keen, 1971: 611–612, fig. 1324).
- remondi*, *Fusus* – Philippi, 1887a: 47 [1887b: 43], pl. 2, fig. 16, non Gabb, 1864. Coquimbo, Chile; A. Rémond & southern Chile; Fr. Javier Ovalle [Pliocene-Pleistocene]. Syntypes, SGO.PI.572 (n = 1, no locality); SGO.PI.596 (n = 1, Coquimbo). *Fusinus remondi* (Philippi, 1887) (Herm, 1969: 141–142, pl. 18, figs. 5a, b, 7; DeVries & Frassinetti, 2003: 125; Snyder, 2003: 173, 278). It appears that a new name is required for Philippi's taxon, which is a junior homonym.
- rhopalicus*, *Fusus* – Philippi, 1887a: 44 [1887b: 41], pl. 2, fig. 3. Navidad, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.573 (labeled as "lectotipo"); SGO.PI.4530–4532 (n = 1 each, labeled as "paralectotipo"). *Fusinus* group (Snyder, 2003: 174, 278).
- rudis*, *Fusus* – Philippi, 1844g: 180, 302, pl. 25, fig. 30. Pezzo near Regium, Santo Mauro & Stilo, Calabria, Italy; fossil. *Fusinus rudis* (Philippi, 1844) (Sabelli et al., 1990: 198).
- schwarzenbergii*, *Fusus* – Philippi, 1844z4: 59, [87], pl. 4, fig. 15, non Speyer, 1863. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Synonym of *Streptochetus cheruscus* (Philippi, 1844) (Tembrock, 1960: 375, 1965b: 432; Janssen, 1978a: 111–112, 1979a: 297–298, pl. 16, fig.



25; Snyder, 2003: 184). Lectotype, PHB MB Ga. 124 (T) 96 (Freden, near Alfeld/Leine, Germany; Late Oligocene), designated by Cadée & Janssen (1994: 46, pl. 1, fig. 10), who noted that “more than 20 specimens of this species were available to Philippi,” but none of the six syntypes in the Berlin collections “matches the height indicated.”

*sowerbyanus*, *Fusus* – Philippi, 1887a: 48–49 [1887b: 45], pl. 3, fig. 16, in part for *Triton leucostomoides* G. B. Sowerby I, 1846. Isla Huafo, Chile; J. Toribio Medina. *Fusinus* group (Snyder, 2003: 189, 282), or a junior synonym of *Urosalpinx leucostomoides* (G. B. Sowerby I, in Darwin, 1846) (Cossmann, 1899: 239, pl. 10, fig. 7).

*spinosa*, *Turbinella* – Philippi, 1845i: 68, *non* Gray 1838. China. Tryon (1881: 96–97) as an “undetermined species of Peristerniinae.”

*strigatus*, *Fusus* – Philippi, 1850j: 116–117 [22–23], pl. 5, fig. 3. Locality unknown. The northeastern South American *Fusinus strigatus* (Philippi, 1850) (Rios, 1994: 132, pl. 42, fig. 570).

*subclavatus*, *Fusus* – Philippi, 1887a: 44 [1887b: 40], pl. 2, fig. 2. Navidad, Chile; Tertiary [Miocene]. Syntype, SGO.PI.580 (n = 1, labeled as “lectotipo”). *Fusinus* group (Snyder, 2003: 195, 283, misspelled as “*F. subclaratus*”).

*umbilicatus*, *Fusus* – Philippi, 1851c: 77. Locality unknown; Largilliert. Status uncertain (Snyder, 2003: 213); Tryon (1881: 68) stated that this “is certainly not a *Fusus*, but the description does not indicate its generic position”.

#### Nassariidae

*acutimargo*, *Buccinum* – Philippi, 1851b: 55–56. China; Largilliert. Tryon (1882a: 62) transferred this species to *Nassa* [= *Nassarius*]; Cernohorsky (1984: 213) listed this as a “dubious Indo-Pacific species of Nassariidae”.

*afrum*, *Buccinum* – Philippi, 1851b: 56. East Africa, Aden (Th. Philippi), Madagascar (Largilliert). Tryon (1882a: 62) transferred this species to *Nassa* [= *Nassarius*]; Cernohorsky (1984: 98–99) stated that this was possibly a senior synonym of *Nassarius* (*Niotha*) *coronulus* (A. Adams, 1852), but absent type material, and given that Dunker’s collection in the ZMB had “2 different species [both] labeled ‘*Buccinum afrum* Philippi’ from Madagascar,” he “found it advisable to retain

the well-documented taxon *N. coronulus* for this species”.

*antillarum*, *Buccinum* – Philippi, 1849h: 139; 1849-l: 42 [2], pl. 1, fig. 2. Cuba; “attulit frater” [= Bernhard Philippi]. Synonym of the western Atlantic *Nassarius vibex* (Say, 1822) (Cernohorsky, 1975a: 147–148, figs. 55, 56).

*bicolor*, *Buccinum* – Philippi, 1851b: 56–57, *non* Megerle von Mühlfeld, 1824. Locality unknown. Tryon (1882a: 62) transferred this species to *Nassa* [= *Nassarius*]; Cernohorsky (1984: 214) listed this as a “dubious Indo-Pacific species of Nassariidae”.

*birmanicum*, *Buccinum* – Philippi, 1851b: 57. Mergui Archipelago, Burma [Myanmar]. Tryon (1882a: 62) transferred this species to *Nassa* [= *Nassarius*]; Cernohorsky (1984: 214) listed this as a “dubious Indo-Pacific species of Nassariidae”.

*bronnii*, *Buccinum* – Philippi, 1849h: 137–138; 1849-l: 49–50 [9–10], pl. 1, fig. 17, *non* Anton, 1839. Java. Synonym of the Indo-Pacific *Nassarius coronatus* (Bruguière, 1798) (Cernohorsky, 1972a: 129–131, figs. 6–9, 21; Wilson, 1994: 80, pl. 14, fig. 2a–d; Higo et al., 1999: 252).

*caperatum*, *Buccinum* – Philippi, 1849u: 68–69 [16–17], pl. 2, fig. 12. Locality not stated. *Niotha caperatum* (Philippi, 1849), or synonym of *Nassarius pauperatus* (Lamarck, 1822) (Tryon, 1882a: 52, 207), although Cernohorsky (1984: 214) stated that “I am unable to associate this taxon with any particular species”.

*cecillii*, *Buccinum* – Philippi, 1848c: 27. Manila, Philippine Islands; Cécille via Largilliert. Tryon (1881: 239) transferred this species to *Nassa* [= *Nassarius*], but subsequently (Tryon, 1882a: 207) listed this as a *Cantharus* [Buccinidae]; Cernohorsky (1984: 214) listed this as a “dubious Indo-Pacific species of Nassariidae”.

*chinense*, *Buccinum* – Philippi, 1851b: 57–58, *non* Dillwyn, 1817. Liew-Kiew, China [Ryukyu Islands, Japan]; Cécile via Largilliert. Tryon (1882a: 62) transferred this species to *Nassa* [= *Nassarius*]; Cernohorsky (1984: 214) listed this as a “dubious Indo-Pacific species of Nassariidae”.

*conspersum*, *Buccinum* – Philippi, 1849h: 138–139; 1849-l: 44–45 [4–5], pl. 1, fig. 6. Canary Islands; Largilliert. *Nassarius conspersus* (Philippi, 1849), Canary Islands and the Selvagens Archipelago (Segers et al., 2008: 19–20).



- corruscans*, *Buccinum* – Philippi, 1851b: 58. Bali; Largilliert. Tryon (1882a: 62) transferred this species to *Nassa* [= *Nassarius*]; Cernohorsky (1984: 214) listed this as a “dubious Indo-Pacific species of Nassariidae”.
- crassum*, *Buccinum* – Philippi, 1849-l: 43–44 [3–4], pl. 1, fig. 4, ex Koch ms, *non* Nyst, 1844, *non* Catlow & Reeve, 1845. China; Largilliert. This species was specifically noted as “in literis”, and Philippi is here considered to be its author. Synonym of *Nassarius* (*Niotha*) *acuticostus* (Montrouzier, in Souverbie & Montrouzier, 1864) (Cernohorsky, 1972a: 151, figs. 51, 52, 63).
- deformis*, *Pleurotoma* – Philippi, 1887a: 40 [1887b: 36–37], pl. 1, fig. 19. Chile; collection of Fr. Javier Ovalle. Syntypes, SGO. Pl.831 (n = 1, labeled as “lectotipo”); SGO. Pl.4526 (n = 1, labeled as “paralectotipo”). Shuto (1992: 22) transferred this to the Nassariidae, as *Bullia* (*Buccianops*) *deformis* (Philippi, 1887).
- escalae*, *Buccinum* – Philippi, 1860a: 188 [1860b: 170], Zool. “pl. 7”, without specifying a figure. Mejillones, Chile. *Nassarius escalae* (Philippi, 1860) (Dall, 1909: 215; Valdovinos, 1999: 139; Letelier et al., 2003: 83), although Cernohorsky (1984: 39) listed this as a “dubious species”.
- gemma*, *Buccinum* – Philippi, 1849-l: 44 [4], pl. 1, fig. 5. Locality unknown; Reents. Synonym of the Panamic *Nassarius complanatus* (Powys, 1835) (Dall, 1909: 287; Cernohorsky, 1975a: 137–138, fig. 37).
- helenae*, *Melania* (*Melanopsis*) – Philippi, 1847d: 170 [20], pl. 4, fig. 4, ex Meder ms. Java. Syntypes, MNHN Paris (n = 5, from Java, ex Meder) (largest, 19.4 mm x 8.2 mm) (the Meder collection was sold in Paris in 1852; the MNHN Paris acquired most or all of it; van der Bijl, 1992: 27–28). *Canidia helenae* (Philippi, 1847) (Schepman, 1912: 236; Benthem Jutting, 1929: 86), or as *Anentome helenae* (Philippi, 1847) (Benthem Jutting, 1959: 107), or as *Clea helenae* (Philippi, 1847) (Brandt, 1974: 201–202, pl. 15, figs. 64–65), often misspelled as “*helenae*” (e.g., Kantor, 2003: 207, fig. 4). Although native to southeast Asia, it is widespread in the freshwater aquarium trade (Bogan & Hanneman, 2013). Recently transferred from the Buccinidae to the Nassariidae, as *Anentome helenae* (Galindo et al., 2016: 341, 348–350).
- laetum*, *Buccinum* – Philippi, 1849h: 140–141. Locality unknown; Reents. Tryon (1882a: 62) transferred this species to *Nassa* [= *Nassarius*]; Cernohorsky (1984: 215) listed this as a “dubious Indo-Pacific species of Nassariidae”.
- limatum*, *Buccinum* – Philippi, 1836a: 220, ex Chemnitz ms. Synonym of *Nassarius lima* (Dillwyn, 1817) (Sabelli et al., 1990: 203), which was based on the same figures in Chemnitz (1781: pl. 188, figs. 1808, 1809).
- limicola*, *Buccinum* – Philippi, 1851b: 59. China; Largilliert. Tryon (1882a: 62) transferred this species to *Nassa* [= *Nassarius*]; Cernohorsky (1984: 215–216) listed this as a “dubious Indo-Pacific species of Nassariidae”.
- livescens*, *Buccinum* – Philippi, 1849h: 135. Manilla, Philippine Islands; Largilliert. The Indo-Pacific *Nassarius* (*Niotha*) *livescens* (Philippi, 1849) (Cernohorsky, 1972a: 143–144, figs. 41, 42, 61; Higo et al., 1999: 253; Okutani, 2000: 440–441, fig. 13; Swennen et al., 2001: 129–130, fig. 438; Gili, 2005).
- noduliferum*, *Buccinum* – Philippi, 1849h: 136–137; 1849-l: 42–43 [2–3], pl. 1, fig. 3. Northern China; Largilliert. Tryon (1881: 261) transferred this species to *Nassa* [= *Nassarius*] and subsequently stated that it was possibly a senior synonym of *Nassarius echinata* (A. Adams, 1852) (Tryon, 1882a: 44). However, Cernohorsky (1984: 215–216) listed this as a “dubious Indo-Pacific species of Nassariidae”.
- nucleolus*, *Buccinum* – Philippi, 1846h: 52; 1849-l: 45 [5], pl. 1, fig. 8. Mazatlán, Sinaloa, Mexico. The Panamic *Nassarius nucleolus* (Philippi, 1846) (Cernohorsky, 1975a: 143).
- panamense*, *Buccinum* – Philippi, 1851b: 61. “Paíta, Panama”; E. B. Philippi. A *Nassarius*, but at present a *nomen dubium* (Keen, 1971: 906; Cernohorsky, 1984: 39).
- paposanum*, *Buccinum* – Philippi, 1860a: 188 [1860b: 169–170], Zool. pl. 7, fig. 19. Paposan, Antofagasta, Chile. *Arcularia paposana* (Philippi, 1860) (Dall, 1909: 214); *Nassarius paposanum* (Philippi, “1845”) (Valdovinos, 1999: 139; Letelier et al., 2003: 83), although Cernohorsky (1984: 39) listed this as a “dubious species”.
- pfeifferi*, *Buccinum* – Philippi, 1844n: 111; 1849-l: 45 [5], pl. 1, fig. 7. Locality unknown. The eastern Atlantic *Nassarius pfeifferi* (Philippi, 1844) (Nicklès, 1950: 104, fig. 182; Sabelli et al., 1990: 199; Landau et al., 2009: 22–23, pl. 4, fig. 7). Segers et al. (2008: 18–19) determined that this species was restricted to the coastal regions of the eastern Atlantic; “records from the Canary Islands and the Selvagens Archipelago are, in our opinion, misidentifications” of *N. conspersus* (Philippi, 1849).



*pingue*, *Buccinum* – Philippi, 1851b: 61–62. Bali; Largilliert. Tryon (1882a: 62) transferred this species to *Nassa* [= *Nassarius*]; Cernohorsky (1984: 216) listed this as a “dubious Indo-Pacific species of Nassariidae”.

*quisquiliarum*, *Buccinum* – Philippi, 1851b: 62–63. China; Largilliert. Tryon (1882a: 62) transferred this species to *Nassa* [= *Nassarius*]; Cernohorsky (1984: 216) listed this as a “dubious Indo-Pacific species of Nassariidae”.

*ringens*, *Buccinum* – Philippi, 1851b: 59–60. Locality unknown. Tryon (1882a: 62) transferred this species to *Nassa* [= *Nassarius*]; species not listed by Cernohorsky (1984: 216).

*sinarum*, *Buccinum* – Philippi, 1851b: 63. Mouth of Yong-Si River, China. *Nassarius* (*Zeuxis*) *sinarus* (Philippi, 1851), from China (Cernohorsky, 1984: 154–155, pl. 31, figs. 10–11, pl. 32, fig. 1). Syntype, ZMB 121033 (Cernohorsky, 1984: pl. 31, fig. 10).

*sturmii*, *Buccinum* – Philippi, 1849h: 135–136; 1849-l: 41–42 [1–2], pl. 1, fig. 1. Caribbean, “ad Novam Aureliam”, Yucatan. Synonym of the western Atlantic *Nassarius vibex* (Say, 1822) (Cernohorsky, 1975a: 147–148, figs. 55, 56).

*taeniolatum*, *Buccinum* – Philippi, 1845i: 69. Islas Chonos, Chile. Possible syntypes, but not same as type locality: SMF 314859 (n = 1) (Chiloe); ZMB 14711 (n = 7) (Magellan). *Nassarius taeniolatus* (Philippi, 1845) (Dall, 1909: 215; Carcelles & Williamson, 1951: 299; Castellanos, 1992b: 22–23, pl. 2, fig. 17; Valdovinos, 1999: 139; Letelier et al., 2003: 83; Ramírez et al., 2003: 262; Nielsen & Valdovinos, 2008: 210, fig. 21), or possibly a synonym of *N. gayii* (Kiener, 1834) (Cárdenas et al., 2008: 219).

*variabile*, *Buccinum* – Philippi, 1836a: xiii, 221–222, 226, pl. 12, figs. 1–7; 1844g: 188, 191; 1844n: 110; 1845z: 450; 1847-l: 76. Sicily, Italy. Also fossil. Doubtful syntypes, PHB MB Ga. \_\_\_\_ (T) 61 (Melappo and Melitello, both ex Philippi, but labeled as “*variabile* var.”). Synonym of *Nassarius cuvierii* (Payraudeau, 1826) (Cernohorsky, 1975a: 158–159, fig. 78; Sabelli et al., 1990: 203). Type species (SD Bucquoy et al., 1882) of *Telasco* H. Adams & A. Adams, 1853.

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“*Nannia*” – Philippi, 1844g: 286. A misspelling of *Nanina* Risso, 1826 (Cernohorsky, 1984: 48).

“*burchardi*, *Buccinum*” – Philippi, 1849u: 69 [17], pl. 2, fig. 14. This species was listed by

Sherborn (1924: 937) as a Philippi name, but the header and signature on the description indicate that it should be credited to Dunker, as noted by Tryon (1882a: 26). Holotype, ZMB 108638 (Cernohorsky, 1981: fig. 14). *Nassarius* (*Plicarcularia*) *burchardi* (Dunker in Philippi, 1849) (Cernohorsky, 1981: 148–151).

“*decollatus*, *Buccinum*” – Philippi, 1844g: 189, 303, pl. 27, fig. 11. Castel, Naples, Italy. This name was given in the synonymy of *Nassarius corniculus* (Olivi, 1792) by Cernohorsky (1984: 49) and Sabelli et al. (1990: 199), but in Philippi it appears only in text in a list of varieties – “*minor*, *lutea*, *parum nitens*, *apice decollata*” – and in the figure caption only as “*var. singularis, decollata*” and was thus never an available name.

#### Melongenidae

*bispinosa*, *Pyrula* – Philippi, 1844d: 94 [2], pl. 1, figs. 7, 8. Locality unknown. The western Atlantic *Melongena bispinosa* (Philippi, 1844) (Clench & Turner, 1956: 180–182, pl. 106).

*crassicauda*, *Pyrula* – Philippi, 1849g: 98. China. *Hemifusus crassicaudus* (Philippi, 1849) (Abbott & Dance, 1982: 176; Higo et al., 1999: 259; Okutani, 2000: 502–503, fig. 2; Qi, 2004: 95, pl. 58E, as “1849”; generic allocation varies).

*kieneri*, *Pyrula* – Philippi, 1849g: 98. Locality not stated. Synonym of the western Atlantic *Busycon perversum* (Linnaeus, 1758) (Abbott, 1974: 223).

*martiniana*, *Pyrula* – Philippi, 1844d: 94–95 [2–3], pl. 1, fig. 9, ex Pfeiffer ms. Locality unknown. Synonym of the western Atlantic *Melongena bispinosa* (Philippi, 1844) (Clench & Turner, 1956: 180–182, pl. 106).

#### Muricidae

*albidus*, *Fusus* – Philippi, 1846p: 119 [13], pl. 3, fig. 5. Locality unknown. Synonym of the Magellanic *Xymenopsis buccineus* (Lamarck, 1816); type material probably lost (Pastorino & Harasewych, 2000: 54–55, figs. 52–56, 75–79, 104, 106).

*amoenum*, *Buccinum* – Philippi, 1849h: 140. Locality unknown; Reents. *Ricinula amoenum* (Philippi, 1849). Bieler & Petit (2012: 24), in their catalog of the publications of the Museum Godeffroy (Hamburg), listed this name as a *nomen nudum* of Schmeltz (1864), but Philippi had originally described



- it in the Buccinidae, and Schmeltz merely transferred it to the Muricidae.
- beckii*, *Murex* – Philippi, 1847z1: 39 [3], pl. 2, fig. 1. Locality unknown. Synonym of the west African *Phyllonotus duplex* (Röding, 1798) (Radwin & D'Attilio, 1976: 88–89, pl. 16, figs. 1, 7).
- boliviana*, *Purpura* – Philippi, 1887a: 57 [1887b: 55], pl. 58, fig. 11. Mejillones, Bolivia [now Chile]. Holotype, SGO.PI.693.
- cancellinus*, *Fusus* – Philippi, 1845i: 67; 1846p: 117–118 [11–12], pl. 3, fig. 2. Strait of Magellan, Chile. Holotype, MNHNS 222 (35.3 mm x 17.2 mm). Synonym of *Xymenopsis subnodosa* (Gray, 1839) (Pastorino & Harasewych, 2000: 55–56, figs. 96–103, 106).
- capito*, *Murex* – Philippi, 1844z4: 60, [87], pl. 4, figs. 19, 20. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. *Boreotrophon capito* (Philippi, 1844) (Janssen, 1979a: 281–282), or as *Hexaplex capito* (Philippi, 1844) (Tembrock, 1962: 120; Janssen, 1978a: 95; Gründel, 1997: 10, pl. 2, fig. 4); type species (OD) of *Eopaziella* Gürs, 2001.
- climacodes*, *Fusus* – Philippi, 1887a: 51 [1887b: 47], pl. 3, fig. 17. Puchoco, Chile; Volckmann. Holotype, SGO.PI.574. *Trophon climacodes* (Philippi, 1887); Miocene (Frassinetti, 2006: 67–68, figs. 12, 13).
- cyclopus*, *Purpura* – Philippi, 1836a: xiii, 219, pl. 11, fig. 26; 1844g: 187. Sortino, Siracusa, Sicily, Italy; fossil. Syntype, PHB MB Ga. 445 (V) 72 (21.6 mm x 15.5 mm).
- decolor*, *Fusus* – Philippi, 1845-l: 68; 1846p: 118 [12], pl. 3, fig. 3. Strait of Magellan & Chonos Islands, Chile. Syntypes, MNHNS 220 (n = 1, 32.6 mm x 20.3 mm) (as “holotype” in Pastorino & Harasewych, 2000: figs. 9–10, but there was no holotype specified in the original description); SMF 314545 (n = 2) (31.7 mm x 17.8 mm; 36.0 mm x 20.9 mm). Synonym of *Xymenopsis muriciformis* (King, 1832) (Pastorino & Harasewych, 2000: 43–52, figs. 1–42, 45–49, 83–95, 105, 106).
- doliaris*, *Monoceros* – Philippi, 1887a: 61 [1887b: 57], pl. 6, fig. 11. La Cueva, Chile; Domeyko; Tertiary [Pliocene]. Syntypes, SGO.PI.495; SGO.PI.500 (labeled as “holotipo”). *Chorus doliaris* (Philippi, 1887) (Herm, 1969: 134, pl. 16, fig. 3, pl. 17, fig. 1; Frassinetti, 2000: 141, pl. 2, fig. 1; Nielsen, 2013: 46–48, fig. 6c–i). DeVries (1997: 133) erroneously stated that SGO.PI.500 was the holotype, but as Nielsen (2013: 48) explained, Philippi's original description was based on two complete specimens collected by Domeyko in La Cueva.
- exigua*, *Pyrula* – Philippi, 1887a: 54–55 [1887b: 51], pl. 3, fig. 19. Lebu, Chile; MacSporran; Tertiary. Syntypes, SGO.PI.728 (n = 1, labeled as “holotipo”); SGO.PI.4554 (n = 1, labeled as “paralectotipo”).
- grandis*, *Monoceros* – Philippi, 1887a: 60–61 [1887b: 57], pl. 5, fig. 4, pl. 6, fig. 5, “var.”. La Cueva & Coquimbo, Chile; Quaternary. Syntypes, SGO.PI.510 (La Cueva, labeled as “holotipo”); SGO.PI.513 (n = 1, Coquimbo, figured specimen) (Nielsen, 2013: 48–49, fig. 6j–s). DeVries (1997: 136) erroneously stated that SGO.PI.510 was the “holotype” but this was not designated as such by Philippi. The Pliocene *Chorus grandis* (Philippi, 1887) (DeVries & Frassinetti, 2003: 126). Nielsen & Valdovinos (2008: 10) determined that the records of Herm (1969: 134–135, pl. 15, figs. 2, 3, 5) of this species were actually referable to *Chorus giganteus* (Lesson, 1830).
- hippocastanum*, *Murex* – Philippi, 1845b: 191–192 [1–2], pl. 1, fig. 2. Peru. Synonym of the Panamic *Hexaplex erythrostomus* (Swainson, 1831) (Keen, 1971: 515–516, fig. 980; Radwin & D'Attilio, 1976: 89, pl. 16, fig. 4).
- incisa*, *Purpura* – Philippi, 1848c: 26. Locality unknown. Tryon (1880a: 178) listed this as a “Doubtful *Purpurae*”.
- inermis*, *Murex cristatus* – Philippi, 1836a: pl. 11, fig. 25. Sicily, Italy. This form name appears only on the plate explanation and is present in the text on pp. 209 only as the variety “*β. Costatus, costis nodulosis inermibus*”. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Bucquoy et al. (1882: 20), as *Murex blainvillei* var. *inermis*. Synonym of *Muricopsis cristata* (Brocchi, 1814) (Radwin & D'Attilio, 1976: 167, pl. 27, fig. 10; Sabelli et al., 1990: 190).
- javanica*, *Purpura* – Philippi, 1848c: 27. Java. ZRC 1996.56, neotype (Straits of Johor, Singapore), designated by Tan & Sigurdsson (1996: 526, figs. 8K, 8L). *Thais (Stramonita) javanica* (Philippi, 1848) (Higo et al., 1999: 213), or as *Indothais javanica* (Philippi, 1848) (Claremont et al., 2013: 93).
- laevis*, *Monoceros* – Philippi, 1887a: 61 [1887b: 57–58], pl. 5, fig. 8. Guayacán, Chile; Tertiary. Syntypes, SGO.PI.503; SGO.PI.505; SGO.PI.508 (designated as lectotype, Nielsen, 2013: 48); SGO.PI.5074–5075. Synonym of the Pliocene *Chorus grandis* (Philippi, 1887) (Herm, 1969: 134–135, pl. 15, figs. 2, 3, 5; Nielsen, 2013: 48–49, fig. 6j–s).



- lamellifer*, *Murex* – Philippi, 1887a: 56 [1887b: 52], pl. 3, fig. 22. Matanzas, Chile; Tertiary.
- lamellosus*, *Fusus* – Philippi, 1836a: xii, 204–205, pl. 11, fig. 30, ex Cristofori & Jan ms, non Borson, 1821. Palermo & Messina, Sicily, Italy. Also fossil. Syntype, SMF 314502 (n = 1) (“Messina, Neapole”) (26.3 mm x 15.7 mm). Synonym of *Coralliophila squamosus* (Antonio Bivona, in Andrea Bivona, 1838) (Bouchet & Warén, 1985: 151, figs. 357–361; Sabelli et al., 1990: 197). Type species (OD) of *Hirtomurex* Coen, 1922. Some authors stated that Philippi’s name was the type species of *Pseudomurex* Monterosato, 1872, by subsequent designation of Dautzenberg, 1927, so that *Pseudomurex* would be a senior synonym of *Hirtomurex* (Bouchet & Warén 1985: 151). However, Jousseume (1880: 335) had previously designated *Murex bracteatus* Brocchi, 1814, as the type species of *Pseudomurex*.
- lividus*, *Fusus* – Philippi, 1845o: 21–22 [9–10], pl. 2, fig. 8. Locality unknown. Synonym of *Lataxiena blosvillei* (Deshayes, 1832) (Reeve, 1847: pl. 6, fig. 23), although Tryon (1881: 69–70) listed this under *Afer* (Buccinidae).
- medinae*, *Purpura* – Philippi, 1887a: 58 [1887b: 54], pl. 5, fig. 13. Navidad, Chile; Tertiary. Holotype, SGO.PI.689. *Purpura medinae* Philippi, 1887; Miocene (Tavera, 1979: 97).
- multilamellosus*, *Murex* – Philippi, 1844g: 182–183, 303, pl. 27, fig. 8. Lamati, Calabria, Italy; fossil. Tryon (1880a: 140, 244) listed this as a synonym of *Trophon barvicensis* (Johnston, 1825); Houart (1981: 16, 27–28) concluded that this species was a *nomen dubium*; otherwise, possibly an older name for *Trophonopsis cossmanni* (Locard 1897). Bouchet & Warén (1985: 137–138) determined that Recent records incorrectly assigned to Philippi’s fossil species were instead referable to *Trophon echinatus* (Kiener, 1840).
- nigrita*, *Murex* – Philippi, 1845b: 191 [1], pl. 1, fig. 1. Pacific coast of Mexico. The Panamic *Muricanthus nigritus* (Philippi, 1845) (Keen, 1971: 522–523, fig. 1001; Abbott & Dance, 1982: 138).
- nodulifera*, *Pyrula* – Philippi, 1887a: 53–54 [1887b: 50], pl. 4, fig. 4. “Tumbez”, Chile; fossil. Syntypes, SGO.PI.716 (n = 1, figured specimen, no locality); SGO.PI.724 (n = 1, Tumbez).
- ochroleuca*, *Pyrula* – Philippi, 1844d: 94 [2], pl. 1, figs. 3–6, ex Menke ms. Chile; E. B. Philippi. Synonym of the Chilean *Xanthochorus cassidiformis* (Blainville, 1832) (Dall, 1909: 290).
- papillosa*, *Ricinula* – Philippi, 1849s: 32. Locality unknown. A doubtful species (Tryon, 1880a: 192).
- porphyroidea*, *Pyrula* – Philippi, 1887a: 55 [1887b: 52], pl. 4, fig. 7. Coquimbo, Chile; Quaternary. Holotype, SGO.PI.721. Synonym of the Pliocene to Recent *Xanthochorus cassidiformis* (Blainville, 1832) (DeVries, 2004: 261–264; Nielsen, 2013: 46, figs. 6a, b).
- pyrulatus*, *Monoceros* – Philippi, 1887a: 61 [1887b: 57], pl. 5, fig. 7. Coquimbo, Chile; Quaternary. Synonym of *Chorus doliaris* (Philippi, 1887) (Herm, 1969: 134, pl. 16, fig. 3, pl. 17, fig. 1; Nielsen, 2013: 46–48, figs. 6c–i).
- quisquilla*, *Pyrula* – Philippi, 1887a: 55 [1887b: 51], pl. 3, fig. 21. Lebu, Chile; Fr. Javier Ovalle; Tertiary. Holotype, SGO.PI.714.
- rugosa*, *Pyrula* – Philippi, 1887a: 54 [1887b: 50–51], pl. 3, fig. 20. “Tumbez”, Chile; Francisco Javier Ovalle; [Cretaceous]. Syntypes, SGO.PI.715 (n = 3). *Pyrula rugosa* Philippi, 1887 (Wilckens, 1904: 216; Bandel & Stinnesbeck, 2000: 769–770), or as *Tudicla rugosa* (Philippi, 1887) (Wetzel, 1930: 69).
- scalaris*, *Pyrula* – Philippi, 1887a: 54 [1887b: 51], pl. 4, fig. 5. Algarrobo, Chile; Cretaceous; Ludwig Landbeck. Syntype, SGO.PI.727 (labeled as “lectotipo”).
- simplex*, *Murex* (*Typhis*) – Philippi, 1841f: 26–27; 1844z4: 26–27, 60, [87], pl. 4, fig. 22, as synonym of *M. cuniculosus* Nyst; 1845z: 450. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. Synonym of *Lyrotyphis* (*Lyrotyphis*) *cuniculosus* (Nyst, 1836) (Janssen, 1979a: 283). Type material lost (R. Janssen, pers. comm., April 2013).
- solidum*, *Buccinum* – Philippi, 1887a: 64–65 [1887b: 61], pl. 6, fig. 12, non Schröter, 1805, non Gravenhorst, 1806, non Reeve, 1846. Guayacán, Chile; Tertiary. Syntypes, SGO.PI.732 (n = 1); SGO.PI.4568 (n = 1). Synonym of *Xanthochorus cassidiformis* (Blainville, 1832) (DeVries, 2004: 261–264; Nielsen, 2013: 46, figs. 6a, b).
- squamulata*, *Pyrula* – Philippi, 1836a: xii, 207, pl. 11, fig. 21; 1844g: 180. Palermo, Sicily, Italy. *Coralliophila bracteata* (Brocchi) var. *brevis* (Blainville, 1832) (Tryon, 1880a: 255), or synonym of *Pseudomurex brevis* (Blainville, 1832) (Priolo, 1964: 185–186 [571–572]).
- squamulosus*, *Fusus* – Philippi, 1836a: xii, 204, pl. 11, fig. 31; 1844g: 178, non Deshayes,



1834. Palermo, Sicily, Italy. Also fossil. Synonym of *Coralliophila squamosus* (Antonio Bivona, in Andrea Bivona, 1838); unnecessarily renamed as *Coralliophila (Hirtomurex) lamellosa longicauda* Settepassi, 1971 (Bouchet & Warén, 1985: 153, 155, figs. 357–361; Sabelli et al., 1990: 197; Snyder, 2003: 191).

*subnodosa*, *Pyrula* – Philippi, 1887a: 55 [1887b: 51–52], pl. 4, fig. 6. Guayacán, Chile; Buchanan; Tertiary. Holotype, SGO.PI.717. Synonym of the Pliocene to Recent *Xanthochorus cassidiformis* (Blainville, 1832) (DeVries, 2004: 261–264; Nielsen, 2013: 46, figs. 6a, b).

*tenuis*, *Monoceros* – Philippi, 1887a: 60 [1887b: 57], pl. 5, fig. 10. Coquimbo, Chile; Quaternary. Syntypes, SGO.PI.507 (labeled as “holotipo”); SGO.PI.511 (n = 3, from Guayacán). Synonym of the Pliocene *Chorus grandis* (Philippi, 1887) (Herm, 1969: 134–135, pl. 15, figs. 2, 3, 5; Nielsen, 2013: 48–49, fig. 6j–s).

*unicarinatus*, *Fusus* – Philippi, 1868: 223–224, non Deshayes, 1835, non J. De C. Sowerby, 1850. Strait of Magellan, Chile; William Acton. *Tromina dispectata* Dell, 1990, nom. nov. Type species (OD) of *Tromina* Dall, 1918 (Radwin & D’Attilio, 1976: 187; Dell, 1990: 208–209, 204, fig. 360; Castellanos, 1992a: 23–24, pl. 3, fig. 28).

*ventrosus*, *Monoceros* – Philippi, 1887a: 61–62 [1887b: 58], pl. 6, fig. 4. Coquimbo & Guayacán, Chile; Tertiary. Syntypes, SGO.PI.520 (n = 1, Coquimbo); SGO.PI.516 (n = 2, Guayacán). Synonym of the Pliocene *Chorus grandis* (Philippi, 1887) (Herm, 1969: 134–135, pl. 15, figs. 2, 3, 5; Nielsen, 2013: 48–49, fig. 6j–s).

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“*carinatus*, *Fusus*” – Error by Castellanos (1992a: 13–14, pl. 3, fig. 37) for *Fusus uncarinatus* Philippi, 1868.

“*echinatus*, *Fusus*” – Philippi, 1836a: xii, 206, pl. 11, fig. 10. As “mihi” for a transfer of *Murex echinatus* J. Sowerby, 1818, to *Fusus* (Sowerby’s species is a junior primary homonym of Brocchi, 1814). Tryon (1880a: 231) and Houart (1981: 15, 37) listed this species, which they credited to Philippi, 1836, as a junior synonym of *Trophonopsis muricatus* (Montagu, 1803).

“*scrobicularus*, *Fusus*” – Philippi, 1846p: 118–119 [12–13], pl. 3, fig. 4. Radwin & D’Attilio, 1976: 138, pl. 21, fig. 2) treated this

as *Urosalpinx scrobiculata* (Philippi, 1846), but the description was signed by Dunker, so it is Dunker’s species.

### Marginellidae

*granum*, *Marginella* – Philippi, 1849s: 27, non Kiener, 1834. Aden, Red Sea; Th. Philippi. *Marginella (Gibberula) granum* Philippi, 1849 (Tryon, 1882b: 43), or not a recognized species (Tomlin, 1917: 269).

*secalina*, *Marginella* – Philippi, 1844g: 197, 303, pl. 27, fig. 19, 19a. Sicily, Italy. For *Volvarina triticea* Lamarck, 1822, sensu Philippi (1836a: 232, pl. 12, fig. 15), non Lamarck, 1822. Syntypes, SMF 313358 (n = 2) (8.0 mm x 3.7 mm; 7.5 mm x 3.7 mm). Synonym of *Volvaria mitrella* (Risso, 1826) (Tomlin, 1917: 297; Sabelli et al., 1990: 208).

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“*minuta*, *Marginella*” – Philippi, 1844g: 197, 303, pl. 27, fig. 23. Listed by Tomlin (1917: 281) and by Sabelli et al. (1990: 208) as if it were a Philippi species, it was instead a misuse of *Marginella minuta* Pfeiffer, 1840, a Cuban species, and itself a junior homonym of *Marginella minuta* Gray, 1826. Philippi’s misuse became the basis for *Marginella philippii* Monterosato, 1878, now *Gibberula philippii* (Monterosato, 1878) (Priolo, 1966: 352 [660]).

### Mitridae

*Dibaphus* – Philippi, 1847z6: 63, pl. 3, figs. 1–3. Type species (M): *Mitra edentula* Swainson, 1823. Recent, Indo-Pacific. Valid subgenus of *Mitra* (Cernohorsky, 1976: 469–470; Higo et al., 1999: 279).

*adansonii*, *Mitra* – Philippi, 1849i: 155. Gabon, Guinea; Largilliert. Synonym of *Mitra (Mitra) nigra* (Gmelin, 1791) (Cernohorsky, 1976: 371–373, pl. 323B; Sabelli et al., 1990: 209).

*bernardiana*, *Mitra filosa* – Philippi, 1850c: 25, 26. Marquesas. Synonym of the Indo-Pacific *Domiporta filaris* (Linnaeus, 1771) (Cernohorsky, 1991: 89–91, pl. B, fig. 8, pl. 82).

*bornii*, *Mitra filosa* – Philippi, 1850c: 25, 26. No locality stated. Synonym of *Domiporta filaris* (Linnaeus, 1771), Indo-Pacific (Cernohorsky, 1991: 89–91, pl. B, fig. 8, pl. 82).

*chiloensis*, *Mitra* – Philippi, 1887a: 72 [1887b: 67], pl. 8, fig. 7. Cueva de Cucao, Chiloé, Chile; Tertiary. Holotype, SGO.PI.863. Pos-



sibly an *Imbricaria*; "it is highly probable that *I. chiloensis* is not an *Imbricaria* and may possibly belong to the Volutomitridae" (Cernohorsky, 1991: 142–143, pl. 142).

*cingulata*, *Mitra* – Philippi, 1850c: 28, *non* Lamarck, 1811. Locality unknown. *Nomen dubium* (Cernohorsky, 1976: 287).

*cucurbitina*, *Mitra* – Philippi, 1850c: 27–28. China "?". A species of *Mitra* (*Nebularia*), but a *nomen dubium* (Cernohorsky, 1976: 287).

*distorta*, *Mitra* – Philippi, 1887a: 72 [1887b: 67], pl. 8, fig. 8. Lebu, Chile; Francisco Javier Ovalle; Tertiary.

*eburnea*, *Mitra* – Philippi, 1850c: 29–30; Philippi, 1851c: 84, *non* Grateloup, 1834. Marquesas; Bernardi. Described twice. Synonym of the Indo-western Pacific *Imbricaria conovula* (Quoy & Gaimard, 1833) (Cernohorsky, 1970: 43; 1991: 137–138, pl. C, fig. 18, pl. 136, figs. 1–4, pl. 137; Cernohorsky, 1991: 138).

*gracilis*, *Mitra filosa* – Philippi, 1850c: 25, 26, *non* W. Wood, 1828, and three other prior uses of *Mitra gracilis*. No locality stated. Synonym of the Indian Ocean-western Pacific *Domiporta praestantissima* (Röding, 1798) (Cernohorsky, 1991: 91–92, pl. B, fig. 9, pl. 83; Higo et al., 1999: 283).

*helvacea*, *Mitra* – Philippi, 1851c: 84–85. China; Gruner. *Nomen dubium* (Cernohorsky, 1976: 290).

*hualpensis*, *Mitra* "?" – Philippi, 1887a: 71 [1887b: 67], pl. 8, fig. 6. Hualpen, Chile; Cretaceous. Holotype, SGO.PI.862.

*kieneri*, *Mitra* – Philippi, 1850c: 22–23. For *M. contracta* Swainson *sensu* Kiener, 1838: 24–25, pl. 9, fig. 25, *non* Swainson, 1820. Locality not stated by either Philippi or Kiener. Syntypes, Museum d'Histoire Naturelle, Geneva (n = 3) (Kiener's specimens of "*M. contracta*," fide Cernohorsky, 1976: 396–397). Synonym of the western Pacific *Mitra* (*Nebularia*) *chrysostoma* Broderip, 1836 (Cernohorsky, 1976: 396–397, pl. 256, figs. 5, 6, pl. 331, figs. 8–10; Higo et al., 1999: 276).

*laevigata*, *Mitra* – Philippi, 1847-I: 78, pl. 10a, fig. 8. Westeregeln, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene; Hallisches Museum. *Mitra laevigata* Philippi, 1847 (Koenen, 1890: 543).

*martini*, *Mitra* – Philippi, 1887a: 71 [1887b: 67], pl. 8, fig. 5; 1897: pl. 3, fig. 3. Ancud; Carlos Martin; Tertiary. Holotype, SGO.PI.864 ("Ranquil (Ancud)"). SGO.PI.865 is not a type, as it was collected after 1887. Nielsen (2013: 42) stated that this species was probably early Miocene, not Pliocene, and rejected

the attempt by Cernohorsky (1976: 361) to synonymize this species with *Mitra orientalis* [Gray,] in Griffith & Pidgeon, 1834.

*pusio*, *Mitra* – Philippi, 1850c: 29; 1851c: 85. Described twice. Locality unknown. Not discussed in Cernohorsky (1976); Tryon (1882a: 235) only listed this in the index, without discussion.

*reevei*, *Mitra* – Philippi, 1850c: 23–25. Zanzibar. Philippi proposed this name for Reeve's (1844: pl. 2, fig. 11) use of *Mitra terebralis* Lamarck, 1811, but both refer to the same species. Synonym of *Mitra* (*Mitra*) *incompta* (Lightfoot, 1786); Reeve's type not traceable (Cernohorsky, 1976: 322–323, pl. 253, fig. 11, pl. 274).

*simplex*, *Mitra* – Philippi, 1845z: 450 [*nomen nudum*], *non* Dunker, 1846.

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"*lactea*, *Mitra*" – Philippi, 1836a: 230. This was noted by Sabelli (1990: 209) as if it were a Philippi species, but it was merely a misuse of *Mitra lactea* Lamarck, 1811.

## Volutidae

*domeykoana*, *Voluta* – Philippi, 1887a: 70 [1887b: 66], pl. 6, fig. 4. Chiloé & Isla Quiriquina, Navidad, Chile; Tertiary [Miocene]. Lectotype, SGO.PI.111 (designated by Stuardo & Villarroel, 1974: 149–151, as *Proscaphella*); SGO.PI.102, SGO.PI.106 (Lebu), SGO.PI.108 (Chiloé), SGO.PI.109 (n = 3, Chiloé), SGO.PI.4555 (n = 1), SGO.PI.4556 (n = 1), paralectotypes. *Miomelon domeykoana* (Philippi, 1887) (del Río & Martínez, 2006: 932), or *Palaeomelon domeykoana* (Philippi, 1887) (Nielsen & Frassinetti, 2007b: 88–89, figs. 5.9–5.14).

*dorbignyana*, *Voluta* – Philippi, 1887a: 70 [1887b: 65], pl. 7, fig. 7. Santa Cruz, Chile; Ramón Vidal Gormáz; Tertiary [Miocene]. Holotype, SGO.PI.104. *Proscaphella dorbignyana* (Philippi, 1887) (Ihering, 1907: 208; Stuardo & Villarroel, 1974: 149, figs. 11a, b), or *Miomelon dorbignyana* (Philippi, 1887) (del Río & Martínez, 2006: 941–942, fig. 15.1).

*fusus*, *Fasciolaria* – Philippi, 1841f: 25; 1844z4: 25, 59, 75, [87], pl. 4, fig. 14. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. Transferred to *Voluta* by Speyer (1862: 117–118, pl. 19, fig. 5). *Scaphella* (*Scaphella*) *siemssenii* (Boll, 1851) (Janssen, 1979a: 300–301, who did not use Philippi's



name on the grounds that it was a secondary junior homonym of *Voluta fusus* Quoy & Gaimard, 1833). Type material lost (R. Jansen, pers. comm., April 2013).

*germari*, *Voluta* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 78–79, pl. 10, fig. 18. Westeregeln, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene; Hallisches Museum. *Voluta labrosa* Philippi, 1847 (Koenen, 1890: 518–519, pl. 37, figs. 7–8).

*gracilis*, *Voluta* – Philippi, 1887a: 70 [1887b: 66], pl. 7, fig. 13, *non* Dillwyn, 1823, *non* Swainson, 1825, *non* W. Wood, 1828, *non* I. Lea, 1833. Santa Cruz, Chile; Ramón Vidal Gormáz; Tertiary [Miocene]. Lectotype, SGO.PI.105 (designated by Stuardo & Villarroel, 1974); paralectotypes (n = 3) not found in February 2014. Dall (1890: 313–315, pl. 9, fig. 4) described *Volutilithes philippiana* from the Recent fauna of Chile, and suggested that this name could also be applied to Philippi's Tertiary species, a suggestion followed by Ihering (1897: 305–306). However, Ihering (1896: 96) had earlier concluded that Dall's Recent species was not conspecific with Philippi's Tertiary species, which Ihering renamed *Voluta gracilior* Ihering, 1896. (The inconsistency in the two Ihering papers is inexplicable; while Ihering (1897: 220) cited the 1896 paper, the 1897 paper did not refer to the renaming in 1896). Parodiz (1996: 227–228) stated that MACN 889 was a syntype lot, but this is merely Ihering's later-collected specimen, not Philippi's original material. *Miomelon gracilior* (Ihering, 1896) (del Río & Martínez, 2006: 934, 937–941, fig. 15.2).

*labrosa*, *Voluta* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 78, pl. 10, fig. 16. Westeregeln, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene; Hallisches Museum. *Scaphella labrosa* (Philippi, 1847), early Oligocene of northern Germany (Rossbach & Carter, 1991: 102).

*obesa*, *Voluta* – Philippi, 1887a: 69 [1887b: 65], pl. 8, fig. 3. Ancud, Chiloé & Isla Huiñimó, Chile; Tertiary [Miocene]. Lectotype, SGO.PI.871 (from Huiñimó; designated by Stuardo & Villarroel, 1974: 153, figs. 9a, b, as *Proscaphella*), paralectotypes, SGO.PI.858 (Huiñimó); SGO.PI.859; SGO.PI.866 (Ancud); SGO.PI.869 (Ancud); SGO.PI.870 (Ancud). *Adelomelon obesa* (Philippi, 1887) (Nielsen & Frassinetti, 2007b: 90–91, fig. 7).

*rugosa*, *Mitra* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 77, pl. 10a, fig. 7, *non* Swain-

son, in G. B. Sowerby I, 1825. Magdeburg area, Germany; Tertiary; Hallisches Museum. Synonym of *Voluta semigranosa* Nyst, 1845 (Cernohorsky, 1972b: 224).

*vidali*, *Voluta* – Philippi, 1897: 367–368, pl. 3, fig. 1. N. of Punta Roble 3 mi. S. of Cabo Quilán, Isla Chiloé, Chile, Miocene. Syntype, SGO.PI.5077. *Pachycymbiola vidali* (Philippi, 1887) (Nielsen & Frassinetti, 2007b: 97, fig. 11.1–15).

#### Olividae

*buchanani*, *Oliva* – Philippi, 1887a: 73 [1887b: 68], pl. 8, fig. 12. Guayacán, Chile; Tertiary [Pliocene]. Syntypes SGO.PI.538 (n = 1); SGO.PI.529 (n = 1). Synonym of *Oliva peruviana* Lamarck, 1811 (Nielsen, 2013: 42, fig. 4e–j).

*coniformis*, *Oliva* – Philippi, 1848d: 53–54 [3–4], pl. 1, figs. 5–7. Locality unknown. Synonym of the Peruvian *Oliva peruviana* Lamarck, 1811 (Zeigler & Porreca, 1969: 31).

*lebuensis*, *Oliva* – Philippi, 1887a: 73 [1887b: 69], pl. 8, fig. 13; 1897: pl. 10, fig. 6. Lebu, Chile; Tertiary [Miocene]. Holotype, SGO.PI.528 (Nielsen, 2004: fig. 16). Synonym of *Olivancillaria claneophila* (Duclos, 1835) (Nielsen, 2004: 89–90, figs. 2–7, 14–18; Griffin & Nielsen, 2008: 309, pl. 24, figs. 10, 11), which occurs from Peru to southern Chile.

*otaeguii*, *Oliva* – Philippi, 1887a: 74 [1887b: 69, as “Oval?”], pl. 8, fig. 21. Hacienda Curauma, Chile; Domingo Otaegui; Tertiary. Holotype, SGO.PI.541 (Nielsen, 2004: figs. 14–15). Synonym of *Olivancillaria claneophila* (Duclos, 1835) (Nielsen, 2004: 89–90, figs. 2–7, 14–18; Griffin & Nielsen, 2008: 309, pl. 24, figs. 10, 11).

*pantherina*, *Oliva* – Philippi, 1848d: 51–52 [3], pl. 1, fig. 1. Locality unknown. Synonym of the Panamic *Oliva julieta* Duclos, 1840 (Zeigler & Porreca, 1969: 31; Keen, 1971: 622–623, fig. 1361).

*platensis*, *Oliva* – Philippi, 1893b: 8, pl. 1, fig. 12. Argentina; Tertiary. Martínez et al. (1998: 44, pl. 15, fig. 33) concluded that given the inadequate nature of the description, this taxon could be referable to either the Olividae or the Volutidae.

*pusilla*, *Oliva* – Philippi, 1887a: 74 [1887b: 69], pl. 8, fig. 15. Navidad; Tertiary [Miocene]. Syntypes, SGO.PI.540 (labeled as “lectotipo”); SGO.PI.4610–4616 (labeled as “paralectotipo”). Synonym of *Lamprodomina dimidata* (G. B. Sowerby I, 1846) (Griffin & Nielsen, 2008: 296, pl. 20, figs. 16–17).



*pyriformis*, *Oliva* – Philippi, 1887a: 73 [1887b: 68], pl. 8, fig. 11. Chile; Francisco J. Ovalle collection; Tertiary [Miocene]. Holotype, SGO.PI.532 (Nielsen, 2004: figs. 17–18). Synonym of *Olivancillaria claneophila* (Duclos, 1835) (Nielsen, 2004: 89–90, figs. 2–7, 14–18; Griffin & Nielsen, 2008: 309, pl. 24, figs. 10, 11).

*subangulata*, *Oliva* – Philippi, 1848d: 51 [1], pl. 1, fig. 2. Pacific Ocean. Syntypes, NHMUK 1924.1.5.98-99 (n = 2) (58.9 mm x 26.1 mm; 59.4 mm x 27.1 mm) (Tursch et al., 1998: 5, 32, pl. 11, fig. 6). Synonym of the Panamic *Oliva spicata* (Röding, 1798) (Zeigler & Porreca, 1969: 33; Keen, 1971: 623–624, fig. 1365).

#### Conidae (*Conus* only)

*ater*, *Conus mediterraneus* – Philippi, 1836a: 238, pl. 12, figs. 20, 21. Pantano del Faro, Messina, Sicily, Italy. Lectotype, the larger of the two specimens figured by Philippi (41 mm x 18 mm), designated by Coomans et al. (1981: 25, fig. 65). Kohn (1992: 265–266, pl. 25, figs. 533, 534), noted that the whereabouts of the lectotype was unknown, but the other specimen illustrated by Philippi (1836, pl. 12, fig. 21) was in the ZMB 10852 (31.7 mm x 12.6 mm), and “must be regarded as a paralectotype.” Additional paralectotype, SMF 313292 (Messina); lot has 4 specimens, but label specifies that only 1 is *ater* (22.9 mm x 11.0 mm), and the other 3 are *franscicanus* Bruguière. Synonym of *Conus ventricosus* Gmelin, 1791 (= *C. mediterraneus* Hwass, 1792) (Coomans et al., 1981: 25; Sabelli et al., 1990: 210; Kohn, 1992: 265–266).

*demissus*, *Conus* – Philippi, 1836a: 239; 1844g: 200, 303, pl. 28, fig. 22 [not cited in text]. Sortino, Sicily, Italy; fossil [Miocene]. Lectotype, PHB MB Ga. 447 (U) 116 (26.8 mm x 18.3 mm), designated by Kohn (1992: 265, pl. 25, fig. 532); paralectotype PHB MB Ga. 447 (U) 116. Kohn noted that this species name had not been used as a valid name during the past 50 years, and “is an unused senior synonym of *C. berghausi* Michelotti, 1847”, so that suppression of Philippi’s name by the ICZN was requested (Kohn, 1991), and obtained, ICZN Opinion 1699 (1993) (“ruled under the plenary power not to be given priority over the specific name of *Conus berghausi* Michelotti, 1847 whenever the two names are considered to be synonyms”).

*humilis*, *Conus* – Philippi, 1836a: xiii [*nomen nudum*], non Salis Marschlins, 1793.

*marmoratus*, *Conus mediterraneus* – Philippi, 1836a: 238–239, pl. 12, figs. 17, 19, 22. Presumably Sicily, Italy. Lectotype, ZMB 10852a (specimen in pl. 12, fig. 22), designated by Kohn (1992: 266, pl. 25, fig. 535); paralectotypes, ZMB 10852b (n = 3) (specimen in pl. 12, fig. 17; specimen in pl. 12, fig. 19 not found). Coomans et al. (1986: 114, fig. 722) designated ZMB 10852c as the lectotype of *Conus mediterraneus* var. *emisus* De Gregorio, 1885, since De Gregorio cited one of the figured specimens of *marmoratus* in Philippi (pl. 12, fig. 19) for *emisus*. However, the specimen figured by Philippi was live-collected (fig. 19 shows a living animal), while ZMB 10852c was not live collected and is encrusted with serpulid polychaete tubes, as both Coomans et al. (1986) and Kohn (1992: 266) noted. Hence, ZMB 10852c was not the figured specimen as cited by either Philippi or De Gregorio, so that the lectotype designation for *emisus* was in error. However, as *emisus* is itself a junior synonym (of *C. ventricosus*), this erroneous designation is of no consequence. Synonym of *Conus ventricosus* Gmelin, 1791 (Kohn, 1992: 266).

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“*brocchii*, *Conus*” – Tomlin (1937: 222) listed this as an 1843 Philippi name (i.e., Philippi, 1844z4: 62), and as a junior homonym of *C. brocchii* Bronn, 1828; but it is merely Philippi’s misidentification of German Oligocene specimens using Bronn’s name, and not a new species. *Conus semperi* Speyer, 1863, is available for *C. brocchii sensu* Philippi, 1844, non Bronn, 1828 (Janssen, 1979a: 329–330, pl. 18, fig. 78).

“*concinnus*, *Conus*” – Tomlin (1937: 231) listed this as an 1847 Philippi name (i.e., Philippi, 1847-l: 80), and as a junior homonym of *C. concinnus* J. De C. Sowerby, 1821; but it is merely Philippi’s misidentification of specimens using Sowerby’s name, and not a new species. *Conus lamarckii* Edwards, 1856, is available for *C. concinnus sensu* Philippi, 1847, non J. De C. Sowerby, 1821.

#### Turridae *sensu lato*

*acutinoda*, *Pleurotoma* – Philippi, 1887a: 37 [1887b: 33–34], pl. 1, fig. 8. Cretaceous of Algarrobo; and Lebu & Tubul; Tertiary. Syntypes, SGO.PI.771 (n = 1, Lebu, labeled as “lectotipo”); SGO.PI.773 (n = 3, Algarrobo); SGO.PI.775 (n = 1, Tubul); SGO.PI.4517 (n =



- 1, Lebu, labeled as “paralectotipo”). Although Philippi described this species from both Cretaceous and late-Tertiary formations, it is unlikely that the same taxon is present in such widely separated formations. *Surcula acutinoda* (Philippi, 1887), Tertiary (Tavera, 1942: 590, fig. 4), or as *Speightia acutinodus* (Philippi, 1887), late Miocene (Shuto, 1992: 22, pl. 2, figs. 7–8).
- bellulum*, *Pleurotoma* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 67, pl. 9, fig. 12. Westeregeln; Hallisches Museum. *Clavacula bellulum* (Philippi, 1847), Oligocene of northern Germany (Koenen, 1890: 431–433, pl. 32, figs. 11–12).
- beyrichii*, *Pleurotoma* – Philippi, 1847-l: 68, pl. 10, fig. 2. Magdeburg area, Germany; Tertiary; Hallisches Museum. *Turricula* (*Orthosulcula*) *beyrichi* (Philippi, 1847), early Oligocene (Latdorfian) of northern Germany (Rossbach & Carter, 1991: 105).
- biplicata*, *Mitra* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 77, pl. 10, fig. 16a, b, *non* Risso, 1826. Westeregeln, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene; Hallisches Museum. Synonym of *Cordieria delucii* (Nyst, 1836) (R. Janssen, pers. comm., April 2013).
- brachystomum*, *Pleurotoma* – Philippi, 1844g: 169, 302, pl. 26, fig. 10. Naples. *Mangelia brachystoma* (Philippi, 1844) (Fretter & Graham, 1985: 522–524, figs. 359, 360), or as *Bela brachystoma* (Philippi, 1844) (Sabelli et al., 1990: 211; Giribet & Peñas, 1997: 52 [14], figs. 48–49, as “*B. brachistoma*”; Mariottini et al., 2008: 4–6; Della Bella et al., 2015: 18–19, figs. 37–44), or as *Sorgenfreispira brachystoma* (Philippi, 1844), from Norway to Morocco (Mariottini et al., 2015: 434, 436–438, figs. 14–17).
- caerulans*, *Pleurotoma* – Philippi, 1844g: 168, 175, 302, pl. 26, fig. 4. Sicily, Italy. Syntypes, MNHNS 173 (n = 5, largest, 9.4 mm x 4.4 mm); SMF 313068 (n = 3) (largest, 9.7 mm x 3.8 mm). *Mangiliella caerulans* (Philippi, 1844) (Sabelli et al., 1990: 213), or as *Cythara caerulans* (Philippi, 1844) (Priolo, 1967: 299–300 [677–678]).
- canaliculatum*, *Pleurotoma* – Philippi, 1845z: 450 [*nomen nudum*].
- capuarum*, *Pleurotoma* – Philippi & Scacchi, in Philippi, 1840a: 68. This is the earliest name for the species that had been erroneously discussed and figured as *Pleurotoma crispatum* Cristofori & Jan, 1832, by Philippi (1836a: 200–201; 1844g: 170–171, pl. 27, fig. 12). Philippi’s figured specimen of “*crispatum* Jan” is PHB MB Ga. 456 (V) 72 (formerly in (T) 10). *Pleurotoma capuarum* is a senior synonym of *P. loprestiana* Calcara, 1841, which was discussed by Bouchet & Warén (1980: 32, figs. 82, 208, 209, as *Drilliola*). Thus: *Microdrillia capuarum* (Philippi & Scacchi, in Philippi, 1840) (Palazzi, 2002). Palazzi (2002) argued that the species name had been misspelled from the intended *P. “caprearum”*, but, however logical, this is not demonstrable from the publication itself and thus cannot be changed (ICZN Code Article 32.5 (1999)).
- costatus*, *Fusus* – Philippi, 1836a: xii, 206, pl. 11, fig. 33. Palermo, Sicily, Italy; fossil. Possible syntypes, PHB MB Ga. 450 (n = 4). Synonym of *Pleurotoma columnae* Scacchi, 1835 (Snyder, 2003: 73). Drillidae, as *Turriclavus* (Cretella et al., 2005: 121).
- darwinii*, *Pleurotoma* – Philippi, 1887a: 39 [1887b: 36], pl. 1, fig. 14. Matanzas, Chile. Holotype, SGO.PI.832 (*fide* Shuto, 1992). *Miraclathurella darwinii* (Philippi, 1887), late Miocene (Shuto, 1992: 22, pl. 1, figs. 20–21).
- decussatum*, *Pleurotoma* – Philippi, 1844g: 174, 302, pl. 26, fig. 23, *non* Couthouy, 1839. Lamati, Calabria & Palermo, Sicily, Italy. Synonym of *Mangelia nuperrima* (Tiberi, 1855) (Bouchet & Warén, 1980: 30–31, 95, figs. 81, 215; Sabelli et al., 1990: 212).
- discors*, *Pleurotoma* – Philippi, 1844z4: 58, [87], pl. 4, fig. 10. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. *Nomen dubium*, or possibly a senior synonym of *Gemmula pseudokonincki* Janssen, 1979 (Janssen, 1979a: 316).
- exilis*, *Pleurotoma* – Philippi, 1849s: 31. Aden, Red Sea; Th. Philippi. *Clathurella exilis* (Philippi, 1849) (Tryon, 1884: 299).
- ferrieri*, *Fusus* – Philippi, 1887a: 43 [1887b: 39], pl. 2, fig. 6. Isla Quiriquina and Hualpen, Chile; Cretaceous. Syntype, SGO.PI.567 (n = 1, labeled as “lectotipo”). Type species (M) of *Struthiolariopsis* Wilckens, 1904 (pp. 208–209, pl. 18, fig. 5). Beu (2011: 94, fig. 15I, 15J) discussed the divergent views taken by authors as to the family for this genus and species, concluded that it “is possibly an early member of the ‘group’ or subfamily Pseudotominae” in the Conoidea, and noted that “Both Philippi’s and Wilckens’ drawings are inaccurate.”
- foncki*, *Pleurotoma* – Philippi, 1887a: 39 [1887b: 36], pl. 1, fig. 15. Lebu, Chile; Tertiary.



- galeritum*, *Pleurotoma* – Philippi, 1844g: 172, 302, pl. 26, fig. 15. Cutro, Calabria, Italy; fossil.
- goldfussii*, *Pleurotoma* – Philippi, 1847-l: 66, pl. 9, fig. 10. Westeregeln, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene; Hallisches Museum. *Clavatula monilifera* (Philippi, 1847) (Koenen, 1890: 422–424, pl. 32, figs. 13–14).
- gracilis*, *Pleurotoma* – Philippi, 1836a: xii, 198, pl. 11, fig. 23, 23a, as *P. gracile*, *non* (Montagu, 1803), *non* Conrad, 1830, *non* Scacchi, 1836. Palermo & Catania, Sicily, Italy.
- granulatum*, *Pleurotoma* – Philippi, 1845z: 450 [*nomen nudum*]; 1847-l: 67, pl. 9, fig. 13. Westeregeln; Tertiary; Hallisches Museum. Synonym of *Clavatula granulata* (Lamarck, 1804), and thus also a junior secondary homonym (Koenen, 1890: 449–451, pl. 34, fig. 12).
- granum*, *Pleurotoma* – Philippi, 1844g: 170, *nom. nov. pro Pleurotoma rude* Philippi, 1836a, *non* “Broderip”, but actually *non* G. B. Sowerby I, 1834, and *non* Scacchi, 1836. Oliverio (1995) redescribed this species. Syntype, ZMB 13779. Synonym of *Clathromangelia quadrillum* (Dujardin, 1837). Type species (M) of *Clathromangelia* Monterosato, 1884.
- grecoi*, *Columbella* – Philippi, 1844g: 194, 303, pl. 27, fig. 18. Pezzo near Rhegium, Calabria, Italy; fossil. Synonym of *Mitrolumna olivoidea* (Cantraine, 1835) (Priolo, 1967: 296–297 [674–675]; Sabelli et al., 1990: 215), or a *nomen dubium* (Amati et al., 2015: 189, 191, 195).
- gruneri*, *Pleurotoma* – Philippi, 1848a: 12–13. St. Thomas, Virgin Islands, 10–15 fms.; Gruner. *Polystira gruneri* (Philippi, 1848) (Todd & Rawlings, 2014: 470, pl. 1, fig. 5).
- hausmanni*, *Pleurotoma* – Philippi, 1844z4: 57, [87], pl. 4, fig. 9. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. *Nomen dubium*, or possibly a senior synonym of *Gemmula pseudokonincki* Janssen, 1979, or of *Pleuroliria koninckii* (Nyst, 1845) (Janssen, 1979a: 316, 317–318, pl. 17, fig. 59).
- hordeum*, *Pleurotoma* – Philippi, 1887a: 39 [1887b: 36], pl. 1, fig. 17. Navidad & Lebu, Chile; Tertiary. Lectotype, SGO.PI.770 (Lebu) (designated by Shuto, 1992: 22); paralectotypes SGO.PI.774 (n = 1, Navidad); SGO.PI.4519–4526 (n = 6, Lebu). Shuto (1992: 22) stated that SGO.PI.4519 was not conspecific with the lectotype, and was possibly referable to *Fusiguraleus*. *Adelocythara hordeum* (Philippi, 1887), late Miocene (Shuto, 1992: 22, pl. 1, figs. 1–3, 17–19).
- jugleri*, *Pleurotoma* – Philippi, 1847-l: 68–69, pl. 10a, fig. 1. Lüneburg; Tertiary. *Epalxis* (*Bathytoma*) *cataphracta jugleri* (Philippi, “1846”) (Anderson, 1964: 287–288, pl. 34, fig. 234; Janssen, 1972: 11); *Bathytoma jugleri* (Philippi, 1847) (Kautsky, 1925: 179–180, pl. 12, figs. 1–2; R. Janssen, pers. comm., April 2013).
- laevigata*, *Pleurotoma* – Philippi, 1836a: xii, 199, pl. 11, fig. 17, 17a, as *P. laevigatum*; 1844g: 169, *non* J. Sowerby, 1823. Catania, Sicily, Italy. Syntypes, SMF 313095 (n = 3) (Catania). Synonym of *Mangelia powisiana* (Dautzenberg, 1887) (Fretter & Graham, 1985: 524–525, fig. 361). *Bela laevigata* (Philippi, 1836) (Sabelli et al., 1990: 211; Giribet & Peñas, 1997: 52 [14]), but Philippi’s name is a primary junior homonym. Priolo (1967: 307 [685]) indicated that *Raphitoma polita* Brusina, 1866, may be the next available name.
- laevis*, *Pleurotoma* – Philippi, 1887a: 39 [1887b: 35], pl. 1, fig. 12, *non* Bellardi, 1848. Lebu, Chile; Tertiary [Miocene]. Syntypes, SGO.PI.772 (Lebu); one other syntype, now lost (S. Nielsen, in litt., 29 Aug. 2014). *Notogenota laevis* (Philippi, 1887), late Miocene (Shuto, 1992: 22), although it requires renaming as Philippi’s name is a junior homonym of Bellardi’s name. Although Shuto (1992: 22) purported to designate a “lectotype” and a “paralectotype” from the SGO.PI collection, his lectotype designation is ineffective, since he did not give a catalog number, or specify which lot was the lectotype.
- laviae*, *Pleurotoma* – Philippi, 1844g: 170, 302, pl. 26, fig. 17, as *P. “LaViae”*, Sicily, Italy. *Raphitoma laviae* (Philippi, 1844) (Sabelli et al., 1990: 215).
- lepida*, *Pleurotoma* “?” – Philippi, 1887a: 40 [1887b: 37], pl. 1, fig. 26. Navidad, Chile; Tertiary. Holotype, SGO.PI.777. Shuto (1992: 22) was unable to determine the current status of this species, due to the poor preservation of the type material.
- leunisii*, *Pleurotoma* – Philippi, 1844z4: 56, [87], pl. 4, fig. 7. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Holotype, PHB MB Ga. 408.1 (T) 17 (not seen in 2013; on loan to Gründel since 1997) (Gründel, 1989: 117, pl. 1, fig. 17). *Bathytoma* (*Bathytoma*) *leunisii* (Philippi, 1844) (Grün-



- del, 1989: 117, pl. 1, fig. 17; Janssen, 1979a: 322, pl. 18, fig. 65; Schnetler & Palm, 2008: 50–51, pl. 7, fig. 13).
- magellanica*, *Daphnella* – Philippi, 1868: 223. Strait of Magellan, Chile; William Acton. *Daphnella magellanica* Philippi, 1868 (Valdovinos, 1999: 140; Letelier et al., 2003: 87).
- maggiori*, *Pleurotoma* – Philippi, 1844g: 175–176, 302, pl. 26, fig. 21 [not cited in text]. Cefali, Catania, Italy; fossil.
- mica*, *Pleurotoma* – Philippi, 1849s: 31. Aden, Red Sea; Th. Philippi. Tryon (1884: 261), in list of names only. *Mangelia mica* (Philippi, 1849) (Issel, 1869: 145, 274).
- milium*, *Mangelia* – Philippi, 1851c: 79–80. China; Largilliert. Tryon (1884: 261), in list of names only.
- moniliferum*, *Pleurotoma* – Philippi, 1847-l: 67–68, pl. 10, fig. 3. Magdeburg area, Germany; Tertiary; Berlin Museum. *Clavatula monilifera* (Philippi, 1847) (Koenen, 1890: 422–424, pl. 32, figs. 13–14).
- nivea*, *Pleurostoma* [sic] – Philippi, 1851c: 92–93. Formosa; Largilliert. The western Indo-Pacific *Tomopleura nivea* (Philippi, 1851) (Higo et al., 1999: 311; Okutani, 2000: 626–627, fig. 37). Neotype, MNHN Paris (the figured lectotype of *Oligotoma makimonos* Jousseume, 1883, a junior synonym of Philippi's species, described from Japan) (27.0 mm x 8.7 mm), designated by Kilburn (1986: 663–664, fig. 62). Type species (OD) of *Tomopleura* T. L. Casey, 1904.
- noduliferum*, *Pleurotoma* – Philippi, 1844g: 173, pl. 26, fig. 16. Between Stilo & Monasterace, Calabria, Italy; fossil.
- obesum*, *Pleurotoma* – Philippi, 1845z: 449 [nomen nudum]; 1847-l: 65, pl. 9, fig. 17. Magdeburg area, Germany; Tertiary; Sack's collection. Koenen (1890: 305) suggested that this species might be a synonym of *Fusus egregius* Beyrich, 1856, and stated that the "Originale von Sülldorf" (near Magdeburg) was in the Dresden Museum.
- perversum*, *Pleurotoma* – Philippi, 1845z: 449 [nomen nudum]; 1847-l: 64–65, pl. 9, fig. 14. Magdeburg area, Germany; Tertiary; Sack's collection. *Pleurotoma perversum* Philippi, 1847 (Koenen, 1890: 365–367, pl. 27, figs. 6–7).
- pygmaeum*, *Pleurotoma* – Philippi, 1844g: 172, pl. 26, fig. 25. Lamati, Calabria, Italy; fossil. A senior primary homonym of *Pleurotoma pygmaeum* C. B. Adams, 1850 (Recent, Jamaica), now classified as *Steironepion pygmaeum* (C. B. Adams, 1850), a genus originally described in the Turridae but now placed in the Columbellidae.
- quisquilia*, *Pleurotoma* – Philippi, 1887a: 39–40 [1887b: 36], pl. 1, fig. 18. Tubul, Araucana, Chile; Tertiary. Holotype, SGO.PI.776. *Mio-wateria quisquilia* (Philippi, 1887), late Miocene (Shuto, 1992: 22, pl. 1, figs. 14–16).
- roemeri*, *Pleurotoma* – Philippi, 1844z4: 56–57. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. *Amblyacrum roemeri* (Philippi, 1844) (Janssen, 1978a: 133), or a *nomen dubium* (Janssen, 1979a: 326).
- rudis*, *Pleurotoma* – Philippi, 1836a: xii, 199, pl. 11, fig. 16, 16a, as *P. rude*, non G. B. Sowerby I, 1834, non Scacchi, 1836. Palermo & Catania, Sicily, Italy. Syntype, ZMB 13779 (n = 1). Philippi's species renamed as *Pleurotoma granum* Philippi, 1844g (q.v.).
- rugulosum*, *Pleurotoma* – Philippi, 1844g: 169, 175, 302, pl. 26, fig. 8; 1844z4: 58. Originally described from the Recent and Pleistocene fauna of Panormitano and Palermo, Sicily (1844g), and later reported from the Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene] (1844z4); the latter publication expressly referred to the Italian specimens. Possible original material of the German Oligocene fossils, PHB MB Ga. 221 & 226 (V) 72 (formerly PHB MB Ga. 221 & 226 (T) 24). The Recent material has been treated as *Clathurella rugulosa* (Philippi, 1844) (Fretter & Graham, 1985: 530–531, fig. 366), or as a synonym of *Mangelia unifasciata* Deshayes, 1835 (Sabelli et al., 1990: 213). The German Oligocene material is now regarded as a distinct species, for which *Amblyacrum roemeri* (Koenen, 1867) is the first available name (Janssen, 1979a: 325–326, pl. 18, figs. 71, 72), although further research is necessary (R. Janssen, in litt., 12 Feb. 2016). Although some authors have dated the Recent species to 1836, Philippi did not use this name for Sicilian material until 1844. Sabelli et al. (1990: 213) noted that this species name was "non (Blainville, 1824)", but we cannot locate the latter. *Pleurotoma rugulosum* Philippi, 1844, is the type species (OD) of *Rugocythara* F. Nordsieck, 1977, now regarded as a junior synonym of *Mangelia* Risso, 1826 (Bouchet et al., 2011: 281).
- scabrum*, *Pleurotoma* – Philippi, 1847-l: 68, pl. 10, fig. 4. Görzig, Sachsen-Anhalt, Germany; Oligocene (Rupelian); Berlin Museum. Type material in PHB MB Ga. \_\_\_\_ (R. Janssen, in



- litt., 9 Feb. 2016; Kautsky, 1925: 190; not found in 2013). Synonym of *Acamptogenotia morreni* (Koninck, 1837) (Janssen, 1979a: 312–313). *Favriella “scraba”* (sic) (Tembrock, 1962: 121).
- secalinum*, *Pleurotoma* – Philippi, 1844g: 170, 302, pl. 26, fig. 9. Sicily, Italy. PHB MB Ga. 459.1, lectotype (8.7 mm x 3.3 mm) (designated by Scarponi et al., 2011: 43–44); paralectotype, PHB MB Ga. 459.2 (7.2 mm x 3.2 mm). *Haedropleura secalina* (Philippi, 1844) (Priolo, 1967: 293–294 [671–672]); Sabelli et al., 1990: 214).
- semilaeve*, *Pleurotoma* – Philippi, 1845z: 449 [nomen nudum]; 1847-l: 66, pl. 9, fig. 15. Westeregeln, Sachsen-Anhalt, Germany; Late Eocene/Early Oligocene; Hallisches Museum. *Clavatula semilaevis* (Philippi, 1847) (Koenen, 1890: 453–456, pl. 31, figs. 3–5).
- simplex*, *Pleurotoma* – Philippi, 1844z4: 57, [87], pl. 4, fig. 8; 1845z: 449; 1847-l: 64, pl. 9, fig. 9, non Deshayes, 1830. *Pleurotoma planispira* Speyer (1866: 19, pl. 3, fig. 3), replacement name. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. Possible syntype, PHB MB Ga. 199. Synonym of *Fusiturris duchastelii* (Nyst, 1836) (Janssen, 1978a: 122–123, 1979a: 318).
- tarentini*, *Pleurotoma* – Philippi, 1844g: 175, 303, pl. 26, fig. 26 [not cited in text]. Lamati, Calabria, Italy; fossil. Syntype, MNHNS 174 (n = 1, 9.5 mm x 3.8 mm). Synonym of *Drilliola loprestiana* (Calcara, 1841) (Priolo, 1967: 295–296 [673–674]; Bouchet & Warén, 1980: 32–33, 94, figs. 82, 208, 209; Sabelli et al., 1990: 214), the latter placing Calcara’s taxon in *Microdrillia*.
- torquatum*, *Pleurotoma* – Philippi, 1844g: 171–172, 302, pl. 26, fig. 14. Between Stilo & Monasterace, Calabria, Italy; fossil.
- undatella*, *Pleurotoma* – Philippi, 1841f: 24; 1844z4: 24, 58, [87], pl. 4, fig. 6. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Nomen dubium*, or possibly either *Asthenotoma obliquinodosa* (Sandberger, 1860), or *Clavus undatellus* (Philippi, 1841) (Tembrock, 1962: 121), or as *Boreodrillia undatella* (Philippi, 1841) (Janssen, 1979a: 322, 325, who stated that since Philippi’s species was a *nomen dubium*, it should date from Speyer, 1867: 197–198, pl. 21, figs. 6–8, but Speyer merely redescribed Philippi’s species, so that Philippi would retain its authorship). Type material lost (R. Janssen, pers. comm., April 2013).
- variegata*, *Pleurotoma* – Philippi, 1836a: xii, 197, pl. 11, fig. 14, as *P. variegatum*. Palermo & Catania, Sicily, Italy. Also fossil. Possible syntypes, SMF 305231 (n = 2) (“Medit.”) (larger, 13.5 mm x 5.7 mm). Synonym of *Philbertia philberti* (Michaud, 1829) (Sabelli et al., 1990: 217).
- vestalis*, *Pleurotoma* – Philippi, 1851c: 93. Locality unknown. An undetermined species (Tryon, 1884: 319).
- volckmanni*, *Pleurotoma* – Philippi, 1887a: 38, 50 [1887b: 35], pl. 1, fig. 10. Tubul & Navidad, Chile; Tertiary. Syntypes, SGO.PI.769 (n = 1, Tubul, labeled as “lectotipo”); SGO.PI.4518 (n = 1, Tubul, labeled as “paralectotipo”). Shuto (1992), not having found the type material, was unable to determine the current status of this species.
- volgeri*, *Pleurotoma* – Philippi, 1847-l: 69, pl. 10a, fig. 2. No locality stated; Oligocene (Rupelian). *Cochlespira volgeri* (Philippi, 1847) (Janssen, 1979a: 313–314; Schnetler & Palm, 2008: 60).
- zimmermanni*, *Pleurotoma* – Philippi, 1847-l: 69–70, pl. 10a, fig. 3a, b. Lüneburg & Eversen an der Aerze [= Örtze] (N of Celle, state of Niedersachsen); Middle Miocene. *Gemmula* (G.) *zimmermanni* (Philippi, 1847) (Janssen, 1972: 11).
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- “*carinatum*, *Pleurotoma*” – Philippi, 1844g: 176, 302, pl. 26, fig. 19. Listed by some authors, such as Schenck (1945: 508), as a Philippi species, it was first made available by Bivona (1838).
- “*inflata*, *Pleurotoma*” – Philippi, 1836a: 197. This was listed by Sabelli et al. (1990: 216) as if it were a Philippi name, but it was only a misuse of *Pleurotoma inflata* Cristofori & Jan, 1832.
- “*obsoleta*, *Mitra*” – Philippi, 1836a: 230. This was listed by Amati et al. (2015: 154, 160) as if it were a Philippi name, “non Brocchi, 1814 nec Bronn, 1831”, and a junior synonym of *Mitromorpha* (*Mitrolumna*) *columbellaria* (Scacchi, 1836). However, as Philippi listed this as *Mitra obsoleta* Brocchi, and he also cited Bronn, then it was only a misuse of Brocchi’s name, not a new species, as Philippi (1844g: 195) himself already recognized in using Scacchi’s name for this Sicilian fossil species.
- “*scraba*, *Favriella*” – Error by Tembrock (1962: 121) for *Pleurotoma scabrum* Philippi, 1847.
- “*striolatum*, *Pleurotoma*” – Philippi, 1844g: 168–169. This is at most a misuse of *Terebra*



*striolatum* Risso, 1826, which Scacchi (1836: 12) transferred to *Pleurotoma*. Sabelli et al. (1990: 212) correctly have Philippi's name as a misuse; they list the Risso species as a synonym of *Mangelia attenuata* (Montagu, 1803), and Philippi's usage as a synonym of *Mangelia nuperrima* (Tiberi, 1855).

"*undatiruga*, *Pleurotoma*" – Philippi, 1844g: 171, 302, pl. 26, fig. 13. Listed by Sherborn (1931: 6725) as described by Philippi, it was actually first made available as *Pleurotoma undatiruga* Antonio Bivona, in Andrea Bivona, 1838.

#### Terebridae

*belcheri*, *Terebra* – Philippi, 1851c: 123–124. Locality unknown; Belcher. Syntypes, SMF 313145 (n = 3) ("Belcher's Reise" ex Hanley) (largest, 41.6 mm x 7.8 mm). Undetermined species (Tryon, 1885a: 40); *nomen dubium* (Bratcher & Cernohorsky, 1987: 29, 229).

*decussata*, *Terebra* – Philippi, 1851c: 124. Locality unknown; Brandt. Undetermined species (Tryon, 1885a: 40); *nomen dubium* (Bratcher & Cernohorsky, 1987: 30, 230).

*subdivisa*, *Terebra* – Philippi, 1851c: 96. Locality unknown. Undetermined species (Tryon, 1885a: 40); *nomen dubium* (Bratcher & Cernohorsky, 1987: 32, 233).

#### Cancellariidae

*australis*, *Cancellaria* – Philippi, 1855a: 208; 1856c: 99; 1856e: 164–165, *non* G. B. Sowerby I, 1832. Strait of Magellan. Syntype, MNHNS 180 (n = 1, 13.9 mm x 8.8 mm). *Admete philippii* Ihering, 1907, replacement name (Forcelli, 2000: 106); *Admete philippii* Carcelles, 1950, an unnecessary additional replacement name.

*exilis*, *Fusus* – Philippi, 1841f: 25–26; 1844z4: 25–26, 60 (misspelled as "*textilis*") [87], pl. 4, fig. 12, *non* Conrad, 1832. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. Synonym of *Babylonella pusilla* (Philippi, 1844) (Janssen, 1978a: 115–117, 1979a: 307–308; Snyder, 2003: 93). Type material lost (R. Janssen, pers. comm., April 2013).

*gracilis*, *Cancellaria* – Philippi, 1845z: 450 [*nomen nudum*] (Petit & Harasewich, 2005: 55).

*medinae*, *Cancellaria* – Philippi, 1887a: 68 [1887b: 63–64], pl. 7, fig. 4. Navidad, Chile; J. Toribio Medina; Tertiary [Miocene]. Lectotype,

SGO.PI.762 (designated by Covacevich & Frassinetti, 1986: 37, pl. 1, fig. 1); paralectotypes, SGO.PI.4527 (pl. 1, fig. 2) (n = 1), SGO.PI.4528 (n = 1). *Cancellaria medinae* Philippi, 1887 (Covacevich & Frassinetti, 1986: 36–43, pl. 1, figs. 1–4; Frassinetti, 2004: 78).

*parva*, *Cancellaria* – Philippi, 1860a: 187 [1860b: 168], Zool. pl. 7, fig. 18, *non* I. Lea, 1833. Paposo, Chile. *Sveltella philippii* Cossmann, 1899, replacement name. However, possibly an *Engina* (Buccinidae) (Petit & Harasewych, 2005: 82).

*pusilla*, *Fasciolaria* – Philippi, 1844z4: 59, [87], pl. 4, fig. 11. Tertiary of Freden & Diekholz, Niedersachsen, Germany [Late Oligocene]. Syntype, RPMH (Hildesheim), from Freden (Janssen, 1979a: 307–308). *Babylonella pusilla* (Philippi, 1844) (Janssen, 1978a: 116–117, 1979a: 307–308; Gründel, 1997: 18, pl. 4, fig. 14; Schnetler & Palm, 2008: 60–61, pl. 6, fig. 2).

*schythei*, *Cancellaria* – Philippi, 1855a: 208; 1856c: 99; 1856e: 164. Strait of Magellan. *Admete schythei* (Philippi, 1855) (Carcelles & Williamson, 1951: 304; Castellanos & Landoni, 1992: 33–34; Valdovinos, 1999: 140; Forcelli, 2000: 106; Letelier et al., 2003: 86; Cárdenas et al., 2008: 222).

*tenera*, *Cancellaria* – Philippi, 1848c: 24–25. Yucatan; Largilliert. The western Atlantic *Ventrilia tenera* (Philippi, 1848). Type species (OD) of *Emmonsella* Olsson & Petit, 1964, which is a junior synonym of *Ventrilia* Jousseume, 1888, as the type species of these two genera are themselves synonyms (Landau et al., 2012: 927–928).

*vidali*, *Cancellaria* – Philippi, 1887a: 68 [1887b: 64], pl. 7, fig. 5. Mouth of Río de Santa Cruz, Patagonia, Chile; Ramón Vidal Gormáz; Tertiary [Miocene]. Holotype, SGO.PI.761. *Cancellaria vidali* Philippi, 1887 (Ihering, 1907: 64; Covacevich & Frassinetti, 1986: 43–45, pl. 1, fig. 5).

#### Acteonidae

*abbreviata*, *Tornatella* – Philippi, 1846q: 23, pl. 2, fig. 1a, b. Near Gossau, Switzerland; Cretaceous.

*acuta*, *Tornatella* – Philippi, 1851c: 125. China; Largilliert. *Solidula acuta* (Philippi, 1851) (Pilsbry, 1894a: 138).

*chilensis*, *Actaeon* – Philippi, 1887a: 111 [1887b: 105–106], pl. 13, fig. 16. Navidad & Matanzas, Chile; Tertiary. *Actaeon chilensis*



Philippi, 1887 (Steinmann & Wilckens, 1908: 12–13, 70).

*landbecki*, *Acteon* – Philippi, 1887a: 111 [1887b: 105], pl. 13, fig. 15. Algarrobo, Chile; Ludwig Landbeck; Cretaceous.

*minutus*, *Actaeon* “?” – Philippi, 1887a: 111–112 [1887b: 106], pl. 13, fig. 17. Navidad; Tertiary [Miocene].

*punctatosulcata*, *Tornatella* – Philippi, 1841f: 20; 1844z4: 20–21, 54, 74, [87], pl. 3, fig. 22, as *T. punctato-sulcata*. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Acteon* (*Acteon*) *punctatosulcatus* (Philippi, 1841) (Speyer, 1870b: 186–188, pl. 20, figs. 6–16; Janssen, 1978a: 147, 1979a: 342, pl. 18a, fig. 99; Rust, 1999: 25, both dated the species from 1843). Possible syntype, PHB MB Ga. \_\_\_\_ (appears to be the figured specimen).

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“*fragilis*, *Tornatella*” – Sherborn (1926: 2506) erroneously listed this species as of Philippi, but the article involved was by Dunker (1846: 169–170), without any species attributed to Philippi.

#### Architectonicidae

*acies*, *Solarium* – Philippi, 1844z4: 74, [87], pl. 3, fig. 32. Tertiary of Luithorst, Niedersachsen, Germany [Late Oligocene]. *Nomen dubium*, or possibly senior synonym of *Architectonica* (*Pseudotorinia*) *bimonilifera* (Sandberger, 1859) (Janssen, 1978b: 182; 2009: 207).

*articulatum*, *Solarium* – Philippi, 1853g: 30. This name appears in a general discussion paragraph concerning varieties of *Solarium perspectiviunculum*, but it is not connected to a description or figure and is thus a *nomen nudum*.

*australe*, *Solarium* – Philippi, 1849i: 168; 1853g: 29, pl. 4, fig. 8. New Zealand, Tahiti; Largilliert. Synonym of the Indo-Pacific *Architectonica perspectiva* (Linnaeus, 1758) (Bieler, 1993: 38–45, pl. 2, fig. A; figs. 23–31).

*australe*, *Solarium* – Philippi, 1887a: 81 [1887b: 76], pl. 9, fig. 12, *non* Philippi, 1849. Navidad, Chile; J. Toribio Medina; Tertiary. Holotype not located; SGO.PI.4999, neotype (designated by Nielsen & Frassinetti, 2007a: 298–299, fig. 4M–Q), the holotype of *H. bahamondei* and type locality thereby restricted to Cerro Los Polos, Navidad Formation, central Chile; late Miocene to early Pliocene. Synonym of

*Heliacus* (*Torinista*) *bahamondei* Frassinetti & Covacevich, 1981.

*bicarinatum*, *Solarium* – Philippi, 1853g: 23–24, pl. 3, fig. 14, *non* Grateloup, 1832. China; Largilliert. *Architectonica kochii* Dall, 1909, *nom. nov.* *Nomen dubium* (Bieler, 1993: 336).

*depressa*, *Solarium perspectiviunculum* – Philippi, 1853g: [30], 41, pl. 4, fig. 10, *non* Grateloup, 1832, *non* Alth, 1850. No locality given. The variety name appears only in the plate explanation. Synonym of *Heliacus* (*Heliacus*) *variegatus* (Gmelin, 1791) (Bieler, 1993: 185; Higo et al., 1999: 353).

*discus*, *Solarium* – Philippi, 1844g: 225, 303, pl. 28, fig. 12; 1853g: 29–30, pl. 4, fig. 9. Naples, Italy. *Discotectonica discus* (Philippi, 1844) (Sabelli et al., 1990: 218; Giannuzzi-Savelli et al., 2014: 12, fig. 2).

*incisum*, *Solarium* – Philippi, 1849i: 168; 1853g: 27–28, pl. 4, fig. 6. Locality unknown. Synonym of *Architectonica perspectiva* (Linnaeus, 1758) (Bieler, 1993: 38–45; see figure citations under *S. australe*).

*maximum*, *Solarium* – Philippi, 1849i: 170; 1853g: 6–7, pl. 1, figs. 2, 3. Based on Chemnitz (1795: pl. 196, figs. 1884, 1885). The Indo-Pacific *Architectonica maxima* (Philippi, 1849) (Abbott & Dance, 1982: 61; Bieler, 1993: 52–56, pl. 1, fig. J, figs. 1, 29–42; Higo et al., 1999: 351; Okutani, 2000: 692–693, fig. 6; Qi, 2004: 133, pl. 79K). Type material not located.

*mediterraneum*, *Solarium luteum* – Philippi, 1853g: 41, pl. 4, fig. 11a–c, as “*mediterranea*”. Mediterranean. This variety name appears only in the plate explanation. Synonym of *Philippia hybrida* (Linnaeus, 1758) (Sabelli et al., 1990: 218). This and the next species are junior homonyms (ICZN Code Article 57.2 (1999)), but as both are also junior synonyms, no renaming is required.

*mediterraneum*, *Solarium stramineum* – Philippi, 1853g: 41 [plate caption], pl. 4, fig. 14a–c, as “*mediterranea*”. Mediterranean. The variety name appears only in the plate explanation. Synonym of *Heliacus* (*Grandelius*) *subvariegatus* (d’Orbigny, 1852) (Sabelli et al., 1990: 218); however, according to Bieler & Petit (2005: 67), the latter is a *nomen nudum*.

*mighelsi*, *Solarium* – Philippi, 1853g: 36–37, unfigured, *nom. nov. pro* *Solarium cyclostomum* Mighels, 1845, *non* Menke, 1830. Oahu, Hawaii. The Hawaiian *Heliacus* (*Teretropoma*) *mighelsi* (Philippi, 1853) (Bieler,



- 1993: 268–270, figs. 219, 220; Higo et al., 1999: 354; Severns, 2011: 398–399, fig. 4).
- modestum*, *Solarium* – Philippi, 1849i: 171; 1853g: 15, pl. 3, fig. 1. Locality unknown. The Indo-Pacific *Architectonica modesta* (Philippi, 1849) (Bieler, 1993: 78–80, pl. 1, fig. E, figs. 57, 62, 63; Higo et al., 1999: 351; Okutani, 2000: 690–691, fig. 3;). Type material not located.
- nanum*, *Solarium* – Philippi, 1853g: 27, pl. 4, fig. 5, ex Koch ms, *non* Grateloup, 1832. Chile. Philippi cited a non-existent article by Koch. Type material not located; *nomen dubium* (Bieler, 1993: 337).
- novaeollandiae*, *Solarium luteum* – Philippi, 1853g: 41, pl. 1, figs. 1, 2, as *S. l.* “*Novae Hollandiae?*”. Presumably Australia. The variety name appears only in the plate explanation. Synonym of *Philippia lutea* (Lamarck, 1822); type material not located (Bieler, 1993: 110–114, figs. 86–89).
- nubilum*, *Solarium* – Philippi, 1849i: 170, ex Menke ms. Cap Haiti. This species was indicated as “in litt.” and thus Philippi is taken to be its author. Synonym of the western Atlantic *Heliacus cylindricus* (Gmelin, 1791).
- pallidum*, *Solarium perspectiviunculum* – Philippi, 1853g: [30], 41, pl. 4, fig. 13, as “*pallida*”. No locality given. This variety name appears only in the plate explanation. Synonym of *Heliacus (Heliacus) areola* (Gmelin, 1791) (Bieler, 1993: 192).
- pictum*, *Solarium* – Philippi, 1849i: 171–172; 1853g: 10, 15–16, pl. 2, fig. 4, pl. 3, fig. 2. Locality unknown. Formerly cited as the Indo-Pacific *Architectonica picta* (Philippi, 1849) (Bieler, 1993: 73–78, pl. 1, fig. B, figs. 57–61); subsequently determined to be a junior synonym of *A. maculata* (Link, 1807) (Bieler & Petit, 2005: 75). Type material not located.
- stellatum*, *Solarium* – Philippi, 1849i: 172; 16–17, pl. 3, fig. 3. Locality not stated. The Indo-Pacific *Architectonica stellata* (Philippi, 1849) (Bieler, 1993: 59–61, figs. 41, 45, 46). Type material not located.
- tricinctum*, *Solarium* – Philippi, 1853g: 36, unfigured. Gabon, Guinea; Largilliert. Philippi cited the “Zeitschr. f. Malakoz. 1851” without a page number for this species, but it did not appear before the 1853 treatment. *Nomen dubium*.
- verrucosum*, *Solarium* – Philippi, 1849i: 172–173; 1853g: 10–11, pl. 2, figs. 5, 6. Locality unknown. Synonym of the eastern Pacific

- Architectonica nobilis* Röding, 1798 (Bieler, 1993: 89–95, figs. 71–73).
- zanclaea*, *Bifrontia* “?” – Philippi, 1844g: 225, 303, pl. 28, fig. 11, 11a. Messina, Sicily, Italy. *Pseudomalaxis zancaeus* (Philippi, 1844) (Sabelli et al., 1990: 219; Giannuzzi-Savelli et al., 2014: 12, fig. 9); the use by some authors of “*zancleus*” is in error. Type species (M) of *Pseudomalaxis* P. Fischer, 1885, a valid genus of the Architectonicidae (Bieler, 1993: 314–315).
- zonatum*, *Solarium* – Philippi, 1849i: 173. Locality not stated. Synonym of *Architectonica perspectiva* (Linnaeus, 1758) (Bieler, 1993: 38–45; see figure citations under *S. australe*).

#### Nerineidae

- roemeri*, *Nerinea* – Philippi, 1837d: 294–295, pl. 3, figs. 1, 2. “Kalksteine Siziliens”.

#### Omalogyridae

- atomus*, *Truncatella* – Philippi, 1841a: 54, 59, pl. 5, fig. 4; 1844g: 134, 301, pl. 24, fig. 5. Sorento, Italy. *Omalogyra atomus* (Philippi, 1841) (Fretter et al., 1986: 221–222, fig. 185; Sabelli et al., 1990: 220; Giribet & Peñas, 1997: 53 [15]; Bieler & Mikkelsen, 1998; Okutani, 2000: 700–701, fig. 3; Kantor & Sysoev, 2005: 167). Type species (SD Tate, 1868) of *Omalogyra* Jeffreys, 1859, as a senior synonym of “*Skenea nitidissima sensu* Forbes & Hanley, 1853” (*non* J. Adams, 1800). Although some authors believed that Philippi’s species was a “bipolar” species found in both northern seas (Arctic Sea and the Black Sea) and the Antarctic (e.g., Marincovich, 1973: 29, fig. 54), Egorova (1991) determined that *Omalogyra atomus* (Philippi, 1841) is limited to the Northern Hemisphere, with the Antarctic specimens instead belonging to *O. antarctica* Egorova, 1991. Valdovinos (1999: 130) erroneously listed both species from Chile.

#### Acididae

- elongatus*, *Pyrgiscus* – Philippi, 1844z4: 53, [87], as *Chemnitzia (Pyrgiscus)*, pl. 3, fig. 10. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. *Nomen dubium*, or possibly a senior synonym of *Aclis (Graphis) hosiusi* (Lienenklaus, 1891) (Janssen, 1978b: 184).



## Pyramidellidae

*Pyrgiscus* – Philippi, 1841a: 50. Type species (SD Dall & Bartsch, in Arnold, 1903): *Melania rufa* Philippi, 1836a. Recent, Mediterranean. See also Philippi (1842g); Schander et al. (1999a: 154). *Ortostelis* Aradas & Maggiore, 1841, has the same type species (SD Dall & Bartsch, 1909: 74). Since the month/dates for these 1841 publications cannot now be determined, the Principle of the First Reviser (ICZN Code Article 24.2 (1999)) has to be applied, and the first authors to use one name as valid and the other as a junior synonym were Dall & Bartsch (1907: 504); they used *Pyrgiscus* as a valid name, with *Ortostelis* as a junior synonym (P. LaFollette, pers. comm. 26 Oct. 2014). Aartsen & Giannuzzi Savelli (1987: 272) incorrectly dated *Ortostelis* to its redescription in 1844 by Aradas & Maggiore.

*acicula*, *Melania* – Philippi, 1836a: xi, 158, pl. 9, fig. 6, 6a. 1844g: 135, as *Eulima*. Palermo, Sicily, Italy; fossil. *Eulimella acicula* (Philippi, 1836) (Priolo, 1960: 93–94 [395–396]; Fekih, 1969: 50, pl. 10, fig. 5, pl. 11, fig. 6; Janssen, 1972: 12; Fretter et al., 1986: 626–627, fig. 436; Sabelli et al., 1990: 223; Peñas et al., 1996: 33, 35, figs. 69, 75; Giribet & Peñas, 1997: 53 [15]; Peñas & Rolán, 1997: 84, 86; Wilke & Aartsen, 1998: 11–12, figs. 6, 21a, 21b; Kantor & Sysoev, 2005: 164; Aartsen & Wesselingh, 2013: 179–180, figs. 4–5; Giannuzzi-Savelli et al., 2014: 118, figs. 291–293 & appendix pp. 35, 82), or a synonym of *Eulimella laevis* (Brown, 1827) (Høisaeter, 2014: 56).

*acicula*, *Turbonilla* – Philippi, 1887a: 96 [1887b: 90], pl. 11, fig. 12. Navidad, Chile; Tertiary [Miocene]. A secondary homonym of *T. acicula* (Lamarck, 1804) at the time of Philippi's publication. Lamarck's species is now the type of *Puposyrnola* Cossmann, 1921; it remains to be determined whether Philippi's species is congeneric with that of Lamarck (P. LaFollette, pers. comm. 9 Dec. 2013).

*affinis*, *Eulima* – Philippi, 1844g: 135, 301, pl. 24, fig. 7. Palermo, Sicily, Italy. Synonym of *Eulimella acicula* (Aradas & Maggiore, 1843) (Tryon, 1886a: 340, pl. 76, fig. 62; who erroneously attributed *acicula* to Philippi), or of *E. ventricosa* (Forbes, 1843) (Priolo, 1960: 97–98 [399–400]), or a valid species, *Eulimella affinis* (Philippi, 1844) (Fekih, 1969: 50, pl. 10, fig. 7).

*areolata*, *Rissoa* – Philippi, 1844g: 132, 301, pl. 23, fig. 23. Reggio & Contrada Carrubara, Calabria, Italy; fossil. Monterosato (1878: 94 [33]) transferred this to the Pyramidellidae, as a possible senior synonym of *Odostomia clathrata* Jeffreys, 1848.

*campanellae*, *Melania* – Philippi, 1836a: xi, 156, pl. 9, fig. 5a, 5b. Palermo & Trepani, Sicily, Italy. Syntypes, SMF 333194 (n = 4); SMF 333195 (n = 5); SMF 305067 (n = 4); possible syntype, PHB MB Ga. \_\_\_\_ (XI) 57 (n = 5) (locality illegible on label). Synonym of *Turbonilla lactea* (Linnaeus, 1758) (Priolo, 1961: 65–68 [405–408]; Sabelli et al., 1990: 226; Peñas & Rolán, 1997: 24–25), or a valid species (Fekih, 1969: 30–31, pl. 5, fig. 6). Philippi's taxon is the type species (SD Dall & Bartsch, 1909) of *Chemnitzia* d'Orbigny, 1840.

*canaliculata*, *Rissoa* – Philippi, 1844g: 223, 303, pl. 28, fig. 19, 19a. Taranto, Italy; fossil. Aartsen (1985) noted confusion between this species and his *Folinella ghisottii* Aartsen, 1984, but said that they are not the same, with the identity of Philippi's species awaiting topotypic material and designation of a neotype; further study is required (Peñas & Rolán, 1998: 20; P. LaFollette, pers. comm. 9 Dec. 2013). Bouchet & Warén (1993: 655–657, figs. 1494–1496, 1502) incorrectly listed this in the synonymy of *Alvania zetlandica* (Montagu, 1815) (Rissoidae), but based solely on Jeffreys (1884: 116).

*clathrata*, *Tornatella* “?” – Philippi, 1836a: xii, 166. Ognina, Catania, Sicily, Italy. Synonym of *Euparthenia humboldti* (Risso, 1826) (Sabelli et al., 1990: 222).

*decorata*, *Odontostomia* – Philippi, 1849s: 29. Red Sea; Th. Philippi & Ehrenberg. Syntype, ZMB 2361 (n = 1). *Chrysallida decorata* (Philippi, 1849) (P. LaFollette, pers. comm. Dec. 2013).

*densecostata*, *Chemnitzia* – Philippi, 1844g: 137, 223, 301, pl. 14, fig. 9. Magnisi Peninsula, Sicily, & Naples, Italy. Synonym of *Turbonilla rufa* (Philippi, 1836) (Sabelli et al., 1990: 227; Peñas & Rolan, 1997: 68, 70), who misspelled it as “*densicostata*”, as did Sherborn (1925: 1842).

*doliaris*, *Odontostomia* – Philippi, 1849s: 29. Aden, Red Sea; Th. Philippi. An undetermined species (Tryon, 1886a: 365), or an *Odostomia* (P. LaFollette, pers. comm. 9 Dec. 2013).

*doliolum*, *Rissoa* – Philippi, 1844g: 132, 301, pl. 23, fig. 19 [not “16” as in text]. Tarenti,



- Sicily, Italy; fossil; also living in Red Sea. Syntype, ZMB 2373 (Red Sea) (n = 1). *Chrysallida doliolum* (Philippi, 1844) (Priolo, 1959: 212–213 [362–363]; Sabelli et al., 1990: 221; Linden & Eikenboom, 1992: 7, figs. 13, 14), now *Odostomella doliolum* (Philippi, 1844) (Schander et al., 1999b: 55, figs. 1–2, 4; Giribet & Peñas, 1997: 53 [15]; Giannuzzi-Savelli et al., 2014: 116, fig. 235 & appendix pp. 27, 74). Type species (OD) of *Odostomella* Bucquoy, Dautzenberg & Dollfus (1883: 158, 167), described as a subgenus of *Odostomia*.
- elongata*, Rissoa – Philippi, 1836a: xi, 154–155, pl. 10, fig. 16; 1844g: 129, 132, *non* Defrance, 1827, *non* Eichwald, 1830. Magnisi Peninsula, Sicily, Italy. Synonym of *Odostomia plicata* (Montagu, 1803) (Priolo, 1960: 86–87 [388–389]; Sabelli et al., 1990: 224).
- elongata*, *Tornatella* – Philippi, 1837c: 292, pl. 3, figs. 4, 5, *non* J. De C. Sowerby, 1836, *non* Grateloup, 1838. Pozzuoli, Naples, or Ischia Id., Italy. Synonym of *Euparthenia bulinea* (Lowe, 1841) (Sabelli et al., 1990: 222).
- erythraea*, *Odontostomia* – Philippi, 1849s: 28–29. Aden, Red Sea; Th. Philippi. An undetermined species (Tryon, 1886a: 365), or placed in *Odostomia* by subsequent authors (P. LaFollette, pers. comm. 9 Dec. 2013), although Aartsen (1987b: 11) considered this to be a *nomen dubium*, and suggested that *Odostomia lorioli* (Hornung & Mermod, 1924) be used instead.
- excavata*, Rissoa – Philippi, 1836a: xi, 154, pl. 10, fig. 6; 1844g: 128, 132. Thapsi [Magnisi] Peninsula, Sicily, Italy. Syntype, SMF 305031 (Magnisi) (n = 1). *Ividella excavata* (Philippi, 1836) (Fretter et al., 1986: 571–573, figs. 388, 389), or as *Folinella excavata* (Philippi, 1836) (Sabelli et al., 1990: 222; Giannuzzi-Savelli et al., 2014: 114, figs. 136–137 & appendix pp. 16, 63), or as *Chrysallida excavata* (Philippi, 1836) (Linden & Eikenboom, 1992: 45–47, figs. 58, 59; Peñas et al., 1996: 18, 29, figs. 60, 61; Giribet & Peñas, 1997: 53 [15]; Peñas & Rolán, 1998: 16, figs. 43–45), or as *Ividella excavata* (Philippi, 1836) (P. LaFollette, pers. comm. 9 Dec. 2013). Type species (SD Dall & Bartsch, 1909) of *Funicularia* Monterosato, 1884 (*non* Forbes 1845 [Cnidaria]), treated by some authors as a synonym of *Chrysallida* Carpenter, 1857.
- gracilis*, *Auricula* – Philippi, 1844z4: 73, [87], pl. 3, fig. 6. Tertiary of Luithorst, Niedersachsen, Germany [Late Oligocene]. *Nomen dubium* (Janssen, 1979a: 338–339), although possibly referable to either *Syrnola subcylindrica* (Philippi, 1844) or to *S. (Puposymola) laevis-sima* (Bosquet, 1859).
- gracilis*, *Chemnitzia* – Philippi, 1844g: 137, 224, 301, pl. 24, fig. 11. Thapsi [Magnisi] Peninsula, Sicily, Italy. *Odostomia delicata* Monterosato, 1874, *nom. nov. pro Chemnitzia gracilis* Philippi, 1844, *non Turbo gracilis* Brocchi, 1814, both of which Monterosato placed in *Odostomia* (both species may actually be referable to *Chemnitzia*, so that the secondary junior homonymy remains; P. LaFollette, pers. comm. 21 July 2015). Sabelli et al. (1990: 222) listed Philippi's species as a synonym of *Euparthyenia bulinea* (Lowe, 1841), and they listed it as if had been originally described as a subspecies of *Chemnitzia humboldti* Risso, 1826. Synonym of *Turbonilla acuta* (Donovan, 1804), Mediterranean and Canary Islands (Peñas & Rolán, 1997: 12), or as a synonym of *Turbonilla delicata* (Monterosato, 1874) (Fekih, 1969: 31–32, pl. 5, fig. 7; Kantor & Sysoev, 2005: 167).
- gracilis*, Rissoa – Philippi, 1844g: 128, 301, pl. 23, fig. 13, *non* Macgillivray, 1843. Thapsi Peninsula, Sicily, Italy. Possibly synonym of *Chrysallida (Parthenia) emaciata* (Brusina, 1866) (Priolo, 1961: 71 [411]), or of *Odostomia interstincta* (Montagu, 1803) (Monterosato, 1872b: 42).
- kochii*, *Pyrgiscus* – Philippi, 1844z4: 53, [87], as *Chemnitzia (Pyrgiscus)*, pl. 3, fig. 7. Tertiary of Freden & Diekholtz, Niedersachsen, Germany [Late Oligocene]. *Nomen dubium*, or possibly a senior synonym of *Turbonilla variculosa* Semper, 1861 (Janssen, 1979a: 340, pl. 18a, fig. 95).
- minuta*, *Pyramidella* – Philippi, 1849s: 32. Aden, Red Sea; Th. Philippi, Hemprich & Ehrenberg. An undetermined species (Tryon, 1886a: 304), or *Niso minuta* (Philippi, 1849) (Issel, 1869: 174).
- obliquata*, *Chemnitzia* – Philippi, 1844g: 137, 301, pl. 14, fig. 10. Thapsi [Magnisi] Peninsula, Sicily, Italy. *Turbonilla obliquata* (Philippi, 1844) (Priolo, 1961: 72 [412]; Sabelli, 1990: 227), or possibly comparable with *Turbonilla sinuosa* (Jeffreys, 1884) (Peñas & Rolán, 1997: 20), or a *nomen dubium* (Giannuzzi-Savelli et al., 2014: 21).
- obtusa*, *Turbonilla* – Philippi, 1887a: 96 [1887b: 91], pl. 11, fig. 13. Navidad, Chile; Tertiary [Miocene].
- pallida*, *Melania* – Philippi, 1836a: xi, 157, pl. 9, fig. 8, 8a; 1844g: 136–137, 138, as *Chemnitzia*. Sicily, Italy. Synonym of *Turbonilla striatula* (Linnaeus, 1758) (Priolo, 1961:



- 80–81 [420–421]; Sabelli et al., 1990: 227), or a valid species, *Pyrgostylus pallidus* (Philippi, 1836) (Fekih, 1969: 47, pl. 8, fig. 4).
- pusilla*, *Chemnitzia* – Philippi, 1844g: 224, 303, pl. 28, fig. 21. Taranto, Italy; fossil. (*Chemnitzia pusilla* C. B. Adams, 1850, a junior homonym of Philippi's species, was renamed *Turbonilla coomansi* Aartsen, 1994.) *Turbonilla pusilla* (Philippi, 1844) (Priolo, 1961: 69–70 [409–410]; Fekih, 1969: 32, pl. 5, fig. 8; Fretter et al., 1986: 636–637, fig. 444; Sabelli et al., 1990: 227; Giribet & Peñas, 1997: 54 [16]; Peñas & Rolán, 1997: 20, 22; Wilke & Aartsen, 1998: 15–16, figs. 15, 30a–c; Daan et al., 2004: 150, fig. 1; Kantor & Sysoev, 2005: 167; Aartsen & Wesselingh, 2013: 182, fig. 19; Giannuzzi-Savelli et al., 2014: 117, figs. 265–267 & appendix pp. 31, 79; (Høisaeter, 2014: 64–65, fig. 107). Type species (OD) of *Cyrtoturbonilla* F. Nordsieck, 1972, which is regarded as a synonym of *Turbonilla*.
- rufa*, *Melania* – Philippi, 1836a: xi, 156, pl. 9, fig. 7, 7a; 1844g: 136, 223, as *Chemnitzia*. Sicily, Italy. Syntypes, ZMB 87446 (n = 3) (Palermo). *Turbonilla rufa* (Philippi, 1836) (Priolo, 1961: 75–77 [415–417]; Fekih, 1969: 36, pl. 6, fig. 6; Sabelli et al., 1990: 227; Peñas et al., 1996: 72, 63, figs. 161, 162; Giribet & Peñas, 1997: 54 [16]; Peñas & Rolán, 1997: 68, 70; Aartsen & Wesselingh, 2013: 183, figs. 23–24; Sysoev, 2014: 153); or *Pyrgiscus rufus* (Philippi, 1836) (Giannuzzi-Savelli et al., 2014: 118, figs. 278–279 & 281–284 & appendix pp. 33, 81; Høisaeter, 2014: 65–66, fig. 108). Type species of *Pyrgiscus* Philippi, 1841 (SD Dall & Bartsch, in Arnold, 1903), of *Ortostelis* Aradas & Maggiore, 1841 (SD Dall & Bartsch, 1909) and of *Pyrgostelis* Monterosato, 1884 (SD Crosse, 1885), all of which some authors now regard as synonyms of *Turbonilla* Risso, 1826.
- scalaris*, *Melania* – Philippi, 1836a: xi, 157, pl. 9, fig. 9, 9a, *non* Spix, in Wagner, 1827, *non* J. de C. Sowerby, 1829; 1841c: 50, as *Pyrgiscus*; 1844g: 137, as *Chemnitzia*. Sicily, Italy. Synonym of *Turbonilla jeffreysii* (Jeffreys, 1848), the next available name (Fretter et al., 1986: 640–642, figs. 447–449; Aartsen, 1987a; Sabelli et al., 1990: 226; Peñas & Rolán, 1997: 53–54; Høisaeter, 2014: 67–68). Aartsen (1987a) noted that other authors have also placed this species in *Parthenia* or in *Ortostelis*. *Melania scalaris* Philippi, 1836, is the type species (OD) of *Pyrgisculus* Monterosato, 1884, a junior synonym of *Pyrgiscus* Philippi, 1841 (Høisaeter, 2014: 65).
- sicula*, *Odostomia* – Philippi, 1851c: 88. Mediterranean. *Odostomia sicula* Philippi, 1851 (Aartsen, 1987b: 11; Sabelli et al., 1990: 225).
- solidula*, *Odontostomia* – Philippi, 1849s: 29–30. Aden, Red Sea; Th. Philippi. *Odontostomia solidula* Philippi, 1849 (Issel, 1869: 179, pl. 2, fig. 2), or as *Odostomia solidula* (Philippi, 1849) (Tryon, 1886a: 365, pl. 79, fig. 88). A senior secondary homonym of *Odostomia solidula* C. B. Adams, 1850.
- striata*, *Rissoa* – Philippi, 1836a: xi, 154, pl. 10, fig. 8, *non* Quoy & Gaimard, 1833. Magnisi Peninsula, Sicily, Italy. Renamed as *Rissoa suturalis* Philippi, 1844g: 129; also renamed later in the same year as *Rissoa mamoi* Aradas & Maggiore, 1844: 137–138, which is a junior synonym (Aartsen & Giannuzzi Savelli, 1987: 272).
- subcylindrica*, *Auricula* – Philippi, 1844z4: 73, [87], pl. 3, fig. 11. Tertiary of Luithorst, Niedersachsen, Germany [Late Oligocene]. Possibly either *Turbonilla* or *Syrnola subcylindrica* (Philippi, 1844) (P. La Follette, pers. comm. 24 Dec. 2013); as *Syrnola subcylindrica* (Philippi, 1844) (Janssen, 1978a: 142, 1979a: 338; Schnetler & Palm, 2008: 63, pl. 8, fig. 7). Speyer (1870a: 59–60, pl. 10, figs. 17–20) erroneously listed this as a junior synonym or variety of *Turbonilla subulata* Merian, 1850, but Philippi's name has precedence.
- subcylindrica*, *Turbonilla* – Philippi, 1887a: 96 [1887b: 91], pl. 11, fig. 14. Navidad, Chile; Tertiary [Miocene]. Secondary junior homonym of *Turbonilla subcylindrica* (Philippi, 1844) (originally described in *Auricula*, and later transferred to *Turbonilla* by some authors); senior homonym of *T. subcylindrica* Schepman, 1909.
- subulata*, *Odontostomia* – Philippi, 1849s: 30. Aden, Red Sea; Th. Philippi. An undetermined species (Tryon, 1886a: 365), or *Odostomia subulata* (Philippi, 1849) (Clessin, 1900: 121, pl. 28, fig. 8).
- suturalis*, *Odontostomia* – Philippi, 1849s: 30. Aden, Red Sea; Th. Philippi. An undetermined species (Tryon, 1886a: 365).
- suturalis*, *Rissoa* – Philippi, 1844g: 129, 132. New name for *Rissoa striata* Philippi, 1836a, *non* Quoy & Gaimard, 1833. *Chrysallida suturalis* (Philippi, 1844) (Fretter et al., 1986: 562–563, fig. 379; Sabelli et al., 1990: 221; Linden & Eikenboom, 1992: 14–15, fig. 22), or as *Parthenina suturalis* (Philippi, 1844), from the eastern Atlantic (Fekih, 1969: 19, pl. 3, fig. 2; Lygre et al., 2011: 478–479, figs.



1C–F; Giannuzzi-Savelli et al., 2014: 116, figs. 182–183 & appendix pp. 21, 68). *Rissoa mamoi* Aradas & Maggiore, 1844, is a junior synonym that has been less frequently used in the recent literature. Sabelli et al. (1990: 221) mistakenly cited the original combination as “*Delphinula suturalis* Philippi, 1844” [sic, pro 1843], which is actually an Oligocene *Solariella*.

*terebellum*, *Chemnitzia* – Philippi, 1844g: 138, 302, pl. 24, fig. 12 [not “2” as in text]. Palermo, Sicily, Italy; fossil. *Chrysallida terebellum* (Philippi, 1844) (Fretter et al., 1986: 563–564, fig. 380; Sabelli et al., 1990: 222; Linden & Eikenboom, 1992: 15–18, figs. 8, 9, 23, 24; Peñas & Rolán, 1998: 44; Wilke & Aartsen, 1998: 11, figs. 5, 20a, 20b; Kantor & Sysoev, 2005: 164), or *Parthenia terebellum* (Philippi, 1844) (Giannuzzi-Savelli et al., 2014: 116, figs. 179–181 & appendix pp. 21, 68). Type species (OD) of *Perparthenina* Nordsieck, 1972.

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“*Odontostoma*” Philippi, 1853a: 192. Probably an unjustified emendation for *Odostomia* Fleming, 1828 (Anonymous, 1853: 317); alternatively, an error for *Odontostomia* Jeffreys, 1839, or a subsequent use of *Odontostoma* Turton, 1830 (P. LaFollette, in litt., 29 Dec. 2014).

“*Odontostomia*” Philippi, 1849s: 28. Although Schander et al. (1999a: 148) thought that this was Philippi’s unjustified emendation for *Odostomia* Fleming, 1813, it is a subsequent use of *Odontostomia* Jeffreys, 1839, itself an emendation of *Odostomia* (P. LaFollette, in litt., 29 Dec. 2014).

“*Orthostelis*” Philippi, 1844g: 287. Error (or emendation) for *Ortostelis* Aradas & Maggiore, 1841 (see under *Pyrgiscus* Philippi, 1841, *supra*).

“*conoidea*, *Auricula*” Vincent, 1886: 10. Erroneously attributed to Philippi and published in synonymy of *Odostomia plicatum* (Montagu, 1803).

“*densestriata*, *Turbonilla*” Brusina, 1865: 23; Brusina, 1866: 69, as “*sensestriata*”. Error for *T. densecostata* Philippi, 1844. Several subsequent authors attributed this name to Brusina, 1866, not Philippi (e.g., Bucquoy et al., 1883: 183; Nordsieck, 1972: 130; Peñas & Rolán, 2000: 76). Regardless of whether this is an error or a *nomen nudum*, the name is invalid, so it is not a senior homonym of *Turbonilla densestriata* Garrett, 1873 (P. LaFollette, pers. comm. 9 Dec. 2014).

“*elegantissima*, *Turbonilla*” Bronn, 1848: 288, 1327 (and others). Also erroneously attributed to Philippi by Brusina, 1865: 23; Kobelt, 1869: 87; and Hörnes, 1856: 499, among others.

#### Amathinidae

*clathratus*, *Fossarus* – Philippi, 1844g: 148, 302, pl. 25, fig. 5, 5a; 1853e: 13–14, pl. 1, figs. 9, 10. Sicily, Italy. *Clathrella clathrata* (Philippi, 1844) (Sabelli et al., 1990: 222; Aartsen & Wesselingh, 2013: 185, fig. 34; Giannuzzi-Savelli et al., 2014: 19, figs. 313–317 & appendix pp. 37, 85). Mienis (1973: 87; 1975: 249) explained that Philippi’s name was the next available name for “*Fossarus*” *costatus* (Brocchi, 1814) and “*Fossarus*” *minutus* (Michaud, 1828), both junior homonyms. Because Brocchi’s taxon is the type species of *Clathrella* Récluz, 1864 (SD Ponder, 1987: 31), the valid name for the type species is Philippi’s name.

#### Ringiculidae

Ringiculidae – Philippi, 1853a: 190. Based on *Ringicula* Deshayes, 1838. Valid family name.

*acuta*, *Ringicula* – Philippi, 1849t: 33. Red Sea, Aden; Th. Philippi. *Ringicula acuta* Philippi, 1849 (Issel, 1869: 173; Pilsbry, 1895a: 405).

*araucana*, *Ringicula* – Philippi, 1887a: 95 [1887b: 90], pl. 11, fig. 10. Lebu, Chile; Tertiary.

*striata*, *Ringicula* – Philippi, 1841f: 28; 1844z4: 28, 61, 76, [87], pl. 4, fig. 23. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Ringicula* (*Ringiculina*) *striata* Philippi, 1841 (Janssen, 1979a: 344–345; Rust, 1999: 25–26, both dated the species from 1843). Possible syntype, PHB MB Ga. 1852 (T) 130.

#### Bullidae *sensu lato*

*acutiuscula*, *Bulla* – Philippi, 1887a: 110 [1887b: 104], pl. 13, fig. 12. Navidad; Tertiary [Miocene]. Syntypes, SGO.PI.797 (n = 1, labeled as “lectotipo”); SGO.PI.4707–4709 (n = 1 each, labeled as “paralectotipo”).

*adansonii*, *Bulla* – Philippi, 1847r: 121. “Senegambia”; Largilliert. *Bullaria adansonii* (Philippi, 1847) (Nicklès, 1950: 136, fig. 279, as *B. “adansonii”*). However, Malaquias & Reid (2008: 463) determined that this was



a junior synonym of *B. striata* Bruguière, 1797.

*hualpensis*, *Bulla* – Philippi, 1887a: 108 [1887b: 102], pl. 13, fig. 11. Hualpen, Chile; Cretaceous. Syntype, SGO.PI.801 (n = 1).

*media*, *Bulla* – Philippi, 1847r: 121. Antilles. Malaquias & Reid (2008: 481) determined that while this species was a potential senior synonym of the well-known *Bulla occidentalis* A. Adams, 1850, it was better treated as a *nomen dubium*, and they concluded: “We recommend reversal of precedence in this case, in order to maintain prevailing usage of the name *B. occidentalis*, but this will require a ruling from the ICZN. Pending an application to the Commission, we maintain usage of the junior synonym (ICZN, 1999: Art. 23.9.3).”

*nesaea*, *Bulla* – Philippi, 1887a: 108 [1887b: 103], pl. 13, fig. 3. Isla Quiriquina, Chile; Cretaceous. Syntypes, SGO.PI.792 (n = 1, labeled as “lectotipo”); SGO.PI.4699, 4700 (n = 1 each, labeled as “paralectotipo”).

*ovulum*, *Bulla* – Philippi, 1887a: 110 [1887b: 104], pl. 13, fig. 4. Navidad, Chile; Tertiary [Miocene]. Holotype, SGO.PI.805.

*panamensis*, *Bulla* – Philippi, 1849h: 114. Panama; E. B. Philippi. Possible senior synonym of *Bulla punctulata* A. Adams, 1850 (Keen, 1971: 793–794, fig. 2236). However, Malaquias & Reid (2008: 497–498) determined that this species was a *nomen dubium*; although potentially a senior synonym of *B. punctulata* A. Adams, 1850, Philippi’s description could not be identified specifically with either a Caribbean or eastern Pacific species.

*plicata*, *Bulla* – Philippi, 1847-l: 59, pl. 9, fig. 5. Magdeburg area, Germany; Tertiary; Sack’s collection. Holotype, Dresden Museum (Koenen, 1892: 955–956). *Acera plicata* (Philippi, 1847), Oligocene of northern Germany (Koenen, 1892: 955–956, pl. 62, fig. 11).

*teretiuscula*, *Bulla* – Philippi, 1845z: 449 [*nomen nudum*]; 1847-l: 58, pl. 9, fig. 3. Magdeburg area, Germany; Tertiary; Sack’s collection. *Cylichna teretiuscula* (Philippi, 1847), Oligocene of northern Germany (Koenen, 1892: 942–945, pl. 61, fig. 6, who stated that the original was in the Dresden Museum).

*triticum*, *Bulla* – Philippi, 1887a: 110 [1887b: 104], pl. 13, fig. 9. Navidad, Matanzas & Lebu, Chile; Tertiary. Syntypes, SGO.PI.802 (n = 1, Lebu, but only one belongs to this species; S. N. Nielsen, 2002 note in collection).

## Haminoeidae

*chilensis*, *Philine* – Philippi, 1887a: 110–111 [1887b: 105], pl. 13, fig. 4. Tumbez, Chile; Ovalle; Cretaceous. *Bulla subglobosa* Philippi, 1887 (Wilckens, 1904: 222, pl. 18, fig. 11).

*exarata*, *Bullaea* – Philippi, 1849h: 141. China; Largilliert. *Bullacta exarata* (Philippi, 1849) (Higo et al., 1999: 398; Qi, 2004: 146, pl. 83P, as “1848”; Malaquias, 2010). Type material not found in ZMB; neotype MNHN Paris 4494 (Tahe-Kiang, China) (14.9 mm x 10.8 mm) (designated by Malaquias, 2010: 2026, fig. 1A, B). Although earlier authors variously classified this species in the Bullactidae, Philinidae or Scaphandridae, Malaquias (2010) concluded that it belonged in the Haminoeidae, with the Bullactidae regarded as a synonym. Senior synonym of *Bulla cauria* Benson, 1856, type species (M) of *Bullacta* Bergh, 1901. It is also the type species (OD) of *Atyscaphander* Annandale, 1924, a junior synonym of *Bullacta*.

*labiosa*, *Bulla* – Philippi, 1851b: 64. China; Largilliert. *Atys labiosa* (Philippi, 1851) (Pilsbry, 1895a: 269; “The generic position is uncertain”).

*pemphis*, *Bulla* – Philippi, 1847r: 122. Red Sea; Gruner. *Haminea pemphis* (Philippi, 1847) (Pilsbry, 1895a: 368, pl. 40, fig. 87). Reeve (1868: *Haminea* pl. 2, fig. 12) and Issel (1869: 168), among others, misspelled this as *Bulla pemphix*.

*perforata*, *Bulla* – Philippi, 1847r: 122. Manila, Philippine Islands; Gruner. *Haminea perforata* (Philippi, 1847) (Pilsbry, 1895a: 370).

*subglobosa*, *Bulla* – Philippi, 1887a: 108 [1887b: 102], pl. 13, fig. 2a, 2b. Isla Quiriquina, Chile; Cretaceous. Syntypes, SGO.PI.804 (n = 1, labeled as “lectotipo”); SGO.PI.4697, 4698 (n = 1 each, labeled as “paralectotipo”). *Bulla subglobosa* Philippi, 1887 (Wilckens, 1904: 222, pl. 18, fig. 11), or as *Atys subglobosa* (Philippi, 1887), Maastrichtian (Wetzel, 1930: 71–72; Bandel & Stinnesbeck, 2000: 776).

## Philinidae

*angustata*, *Bullaea* – Philippi, 1836a: x, 121, pl. 7, fig. 17a–d, ex Bivona ms. Palermo, Sicily, Italy. Also fossil. Synonym of *Philine catena* (Montagu, 1803) (Ohnheiser & Malaquias, 2013: 280–281).

*magellanica*, *Philine* – Philippi, 1887a: 111 [1887b: 105], pl. 13, fig. 5. Skyring Water; Enrique Ibar; Tertiary.



*schroeteri*, *Bullaea* – Philippi, 1844g: 94–95, footnote, 301, pl. 20, fig. 2. Sicily? Synonym of *Philine aperta* (Linnaeus, 1767) (Priolo, 1968: 361–363 [755–757]; Sabelli et al., 1990: 232).

*terebelloides*, *Bulla* – Philippi, 1841f: 18–19; 1844z4: 18–19, [87], pl. 3, fig. 5. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. *Crenilabium terebelloides* (Philippi, 1841) (Kautsky, 1925: 202; Anderson, 1964: 331–332, pl. 50, figs. 297, 297a; Janssen, 1978a: 148, 1979a: 343, pl. 18a, fig. 101, the latter two both dated the species from 1843). Type material lost (R. Janssen, pers. comm., April 2013).

*vestita*, *Bulla* – Philippi, 1840a: 68–69; 1844g: 95, 301, pl. 20, fig. 4, 4a. Sicily, Italy. Previously considered a junior synonym of *Philine retifera* (Forbes, 1844) (Sabelli et al., 1990: 233; Linden, 1995: 75–78, figs. 19, 24, 25; Ohnheiser & Malaquias, 2013: 309–310), it is the senior synonym, by four years. *Philine (Johania) vestita* (Philippi, 1840) (Priolo, 1968: 354–355 [748–749], who dated this species as 1844).

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“*planciana*, *Bullaea*” – Philippi, 1844g: 94, 301, pl. 20, fig. 3, as “*mihi*” but made available by Lamarck, 1801.

#### Cyclichnidae

*brevicula*, *Bulla* – Philippi, 1887a: 110 [1887b: 104], pl. 13, fig. 8. Navidad & Matanzas, Chile; Tertiary. Syntypes, SGO.PI.800 (n = 2, Navidad, but one specimen is Naticidae); SGO.PI.803 (n = 4). *Scaphander brevicula* (Philippi, 1887) (Frassinetti, 2001: 86, figs. 18–19; 2004: 78).

*dilatata*, *Bulla* – Philippi, 1845z: 449 [*nomen nudum*]; 1847-l: 59, pl. 9, fig. 6. Magdeburg area, Germany; Tertiary; Sack’s collection. Koenen (1892: 957–959) stated that the holotype, a steinkern, was in the Dresden Museum. *Scaphander dilatata* (Philippi, 1847) (Koenen, 1892: 957–959, pl. 59, figs. 26–27; R. Janssen, pers. comm., April 2013).

*granulum*, *Bulla* – Philippi, 1851b: 63–64. China; Largilliert. *Cylichna granulum* (Philippi, 1851) (Pilsbry, 1895a: 309).

*lineata*, *Bulla* – Philippi, 1841f: 18; 1844z4: 18, [87], pl. 3, fig. 2, *non* Gray, 1825, *non* Wood, 1828. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. Synonym of *Cylichna sternbergensis* (Boll, 1846) (Janssen, 1979a: 345–346, pl. 18a, fig. 103). Type

material lost (R. Janssen, pers. comm., April 2013).

*mucronata*, *Bulla* – Philippi, 1849r: 22. Red Sea; Th. Philippi. *Acteocina mucronata* (Philippi, 1849) (Sabelli et al., 1990: 234); introduced into the Mediterranean (Aartsen et al., 1990).

*remondi*, *Bulla* – Philippi, 1887a: 109–110 [1887b: 103–104], pl. 13, fig. 7. Navidad, Matanzas, Tubul & Lebu, Chile; Tertiary & “Tumbez”. Syntypes, SGO.PI.791 (n = 1, Tumbez); SGO.PI.795 (n = 9, Lebu); SGO.PI.799 (n = 1, Navidad, labeled as “lectotipo”); SGO.PI.4701–4706 (Navidad, labeled as “paralectotipo”). *Scaphander remondi* (Philippi, 1887); Miocene (Tavera, 1979: 94; Frassinetti, 2001: 86).

#### Retusidae

*apicina*, *Bulla* – Philippi, 1845z: 449 [*nomen nudum*]; 1847-l: 59, pl. 9, fig. 4. Magdeburg area, Germany; Tertiary; Sack’s collection. *Volvula apicina* (Philippi, 1847) (Koenen, 1892: 938–939, pl. 61, figs. 1–3), or as *Volvulella apicina* (Philippi, 1847) (R. Janssen, pers. comm., April 2013), Oligocene of northern Germany.

*cecillii*, *Bulla* – Philippi, 1844z: 164–165. China; Largilliert. Syntypes, SMF 305143 (n = 4). *Retusa cecillii* (Philippi, 1844) (Pilsbry, 1895a: 222, pl. 23, fig. 53).

*intermedia*, *Bulla* – Philippi, 1841f: 18; 1844z4: 18, 51, [87], pl. 3, fig. 4; 1847-l: 58–59, pl. 7, fig. 7a–c. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]; Sack’s collection. *Retusa (Cylichna) laurenti intermedia* (Philippi, 1841) (Janssen, 1979a: 349–350, who dated the subspecies from 1843). However, because Bosquet’s *laurenti* dates from 1859, the sequence of the species and subspecies should instead be *intermedia laurenti*. Type material lost (R. Janssen, pers. comm., April 2013).

*involuta*, *Bulla* – Philippi, 1851b: 64. China; Largilliert. *Retusa involuta* (Philippi, 1851) (Pilsbry, 1895a: 228–229; “The generic position is very doubtful. Perhaps it is a *Cylichna*”).

*mammillata*, *Bulla* – Philippi, 1836a: x, 122–123, pl. 7, fig. 20a–c; 1844g: 96, 97. Trapani, Sicily, Italy. Syntype, ZMB 710 (Magnisi) (n = 1). *Retusa mammillata* (Philippi, 1836) (Priolo, 1968: 340–341 [734–735]; Sabelli et al., 1990: 229). Type species (OD) of *Mamilloretusa* F. Nordsieck, 1972, a synonym of *Retusa* Brown, 1827.



*retusa*, *Bulla* – Philippi, 1841f: 18; 1844z4: 18, [87], pl. 3, fig. 3. Tertiary near Wilhelmshöhe, Hessen, Germany [Late Oligocene]. Synonym of *Retusa (Retusa) minuta* (Deshayes, 1824) (Speyer, 1870b: 174–175, pl. 19, fig. 1; Janssen, 1979a: 349). Type material lost (R. Janssen, pers. comm., April 2013).

*seminulum*, *Bulla* – Philippi, 1851b: 64. Manila, Philippine Islands. *Retusa seminulum* (Philippi, 1851) (Pilsbry, 1895a: 229).

*semisulcata*, *Bulla* – Philippi, 1836a: x, 123; pl. 7, fig. 19a–c [not cited in text]. Sicily, Italy. Syntypes, SMF 305146 (n = 3) (Magnisi, Sicily). *Retusa semisulcata* (Philippi, 1836) (Sabelli et al., 1990: 229; Giribet & Peñas, 1997: 54 [16]), or synonym of *Retusa truncatula* (Bruguière, 1792) (Kantor & Sysoev, 2005: 173).

*teres*, *Bulla* – Philippi, 1851b: 65. Locality unknown. *Tornatina teres* (Philippi, 1851) (Pilsbry, 1895a: 196).

#### Cavoliniidae

“*uncinata*, *Hyalaea*” – Philippi, 1836a: ix, 101, pl. 6, fig. 18, ex Höninghaus ms. This species was first made available as *Hyalaea uncinata* Rang, 1829, now regarded as a valid species of *Cavolinia*. Philippi’s material is now MNHNS 175 (n = 2).

#### Limacinidae

*Scaea* – Philippi, 1844g: 164. Type species (SD Herrmannsen, 1848): *Trochus lunaris* Gmelin, 1791. Recent, Mediterranean. Synonym of *Limacina* Bosc, 1817. Misspelled as *Scea* by Scudder (1882: 301).

*stenogyra*, *Scaea* – Philippi, 1844g: 164, 302, pl. 25, fig. 20, 20a. Palermo, Sicily, & Pezzo, Rhegium, Calabria, Italy, all fossil. Synonym of either *Limacina retroversa* (Fleming, 1823) or of *Limacina trochiformis* (d’Orbigny, 1835) (Sabelli et al., 1990: 238–239).

#### Clionidae

*promaucana*, *Clio* – Philippi, 1887a: 112 [1887b: 106], “pl. 13, fig. 18” [but not on plate]. Navidad, Chile; Tertiary. *Clio promaucana* Philippi, 1887, Miocene (Frassinetti, 2000: 148–149, pl. 2, fig. 22).

#### Aplysiidae

*deperdita*, *Aplysia* – Philippi, 1844g: 99–100, based on 1836a: pl. 7, fig. 10. Palermo, Sicily,

Italy; fossil. Possible syntype, PHB MB Ga. 456 (□) 42 (missing in 2013).

*grandis*, *Aplysia* “?” – Philippi, 1844g: 100, 300, pl. 18, fig. 10a, 10b. Palermo, Sicily, Italy; fossil.

*punctatus*, *Notarchus* – Philippi, 1836a: x, 255–256, pl. 7, fig. 9; 1844g: 100. Panormitano, Sicily, Italy. The eastern and western Atlantic *Notarchus punctatus* Philippi, 1836 (Sabelli et al., 1990: 249; Redfern, 2013: 277, fig. 722).

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“*lepus*, *Aplysia*” – Philippi, 1844g: 99, 301, 301, pl. 22, fig. 3. Listed as “n. sp.”, this was instead a transfer of *Dolabella lepus* Risso, 1826, to *Aplysia*.

#### Placobranchidae

*fusca*, *Elysia* – Philippi, 1844g: 100–101, 301, pl. 22, fig. 4. Palermo, Sicily, Italy. Synonym of *Elysia viridis* (Montagu, 1804) (Schmekel & Portmann, 1982: 279–281, pl. 17, fig. 6; text-fig. 7.94; Sabelli et al., 1990: 242).

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“*Rhycobranchum*” – Philippi, 1844g: 101. Incorrect subsequent spelling of *Rhyzobranchus* Cantraine, 1835; Philippi’s usage is the accusative form of “*Rhycobranchus*” which is still in error.

“*Rhizobranchus*” – Philippi, 1853a: 279. Emendation for *Rhyzobranchus* Cantraine, 1835.

#### Tylodinidae

*rafinesquii*, *Tylodina* – Philippi, 1836a: x, 114, pl. 7, fig. 8a, 8b [not cited in text]; 1844g: 89. Catania, Sicily, Italy. Synonym of *Tylodina perversa* (Gmelin, 1791) (Sabelli et al., 1990: 245, with “*T. rafinesqui*” erroneously credited to Locard, 1886).

#### Pleurobranchidae

*brevifrons*, *Pleurobranchus* – Philippi, 1844g: 87–88, 301, pl. 20, fig. 5a–d. Sicily, Italy. Synonym of *Berthella plumula* (Montagu, 1803) (Sabelli et al., 1990: 246; Thompson, 1976: 167, fig. 94, pl. 21-C).

*mammillatus*, *Pleurobranchus* – Philippi, 1836a: x, 112–113, ex Schultz ms, *non* Quoy & Gaimard, 1832; 1844g: 86, as “*P. mammillatus*” and as a synonym of *P. testudinarius* Cantraine, 1835. Palermo, Sicily, Italy.



*perforatus*, *Pleurobranchus* – Philippi, 1844g: 87, 301, pl. 21, fig. 2, 2a. Catania. Synonym of *Berthella plumula* (Montagu, 1803) (Sabelli et al., 1990: 246; Thompson, 1976: 167–168, fig. 94, pl. 21-C).

#### Chromodorididae

*albescens*, *Doris* – Philippi, 1836a: ix, 105, ex Schultz ms; 1844g: 79, 300, pl. 19, fig. 7. Palermo, Sicily, Italy. Synonym of *Felimida purpurea* (Risso, in Guérin, 1831) (Schmekel & Portmann, 1982: 61–62, pl. 1, fig. 6; text-fig. 7.4; Cattaneo-Vietti et al., 1990: 66–67, pl. 2, fig. 8; Sabelli et al., 1990: 254 (all as *Chromodoris*); current genus: Johnson & Gosliner, 2012: 9).

*elegantula*, *Doris* – Philippi, 1844g: 80, 300, pl. 19, fig. 8, 8c. Palermo, Sicily, Italy. Neotype, Museo Nacional de Ciencias Naturales, Madrid, MNCN 15.05/60113N (designated by Ortigosa et al., 2014b: 546). *Chromodoris elegantula* (Philippi, 1844), endemic to the Mediterranean (Schmekel & Portmann, 1982: 57–58, pl. 6, fig. 4; Cattaneo-Vietti et al., 1990: 60–61, pl. 3, fig. 4; Sabelli et al., 1990: 253), or as *Felimida elegantula* (Philippi, 1844) (Ortigosa et al., 2013, 2014b).

*picta*, *Doris* – Philippi, 1836a: ix, 105; 1844g: 80, 300, pl. 19, fig. 10, as “*D. elegans picta*”, ex Schultz ms. Palermo, Sicily, Italy. Neotype, MNHN Paris (designated by Ortea et al., 1996: 43). *Hypselodoris picta* (Philippi, 1836) (Ortea et al., 1996: 43–57, figs. 10, 28–37), or as *Felimare picta* (Philippi, 1836) (Johnson & Gosliner, 2012: 10 & Table S2; Ortigosa et al., 2014a; Furfaro et al., 2016).

#### Dendrodorididae

*reticulata*, *Doris* – Philippi, 1836a: ix, 105, ex Schultz ms; Philippi, 1844g: 215, *non* Quoy & Gaimard, 1832. Palermo, Sicily, Italy. Synonym of *Doriopsila areolata* Bergh, 1880; Zoologisk Museum Copenhagen GAS-234, neotype (designated by Valdés & Ortea, 1997: 241–248, figs. 1, 2A, 3A, 4, 5).

#### Goniodorididae

*cirriger*, *Euplocamus* – Philippi, 1839a: 115; 1844g: 77, 300, pl. 19, fig. 4, as *Idalia cirrigera*. Neapolitan Sea. Synonym of *Okenia elegans* (Leuckart, 1828) (Sabelli et al., 1990: 250; Thompson & Brown, 1984: 43–44, pl. 11a–d).  
*laciniosus*, *Euplocamus* – Philippi, 1841a: 57–59, pl. 5, fig. 9; 1844g: 77, 300, pl. 19, fig.

5a, 5b, as *Idalia laciniosa*. Naples. Synonym of *Okenia elegans* (Leuckart, 1828) (Sabelli et al., 1990: 250; Thompson & Brown, 1984: 43–44, pl. 11a–d).

#### Polyceridae

*Euplocamus* – Philippi, 1836a: ix, 103–104, *non* Latreille, 1809 [Lepidoptera]. Type species (SD Herrmannsen, 1847 – 1 April): *Doris clavigera* O. F. Müller, 1776. Genus renamed *Kaloplocamus* Bergh, 1892; later also unnecessarily renamed *Heteroplocamus* Oliver, 1915. The type fixation by Gray (1847) of *Euplocamus croceus* Philippi, 1836, was not published until November 1847, that is, eight months later. *Doris clavigera* is also the type species of *Limacia* O. F. Müller, 1781, which would make *Euplocamus* and its replacement names objective synonyms of *Limacia* and require a new genus for the species formerly grouped in *Kaloplocamus*, a name in current use (Vallès & Gosliner, 2006: 179–180). Alternatively, a petition could be submitted to the ICZN to conserve *Kaloplocamus* by setting aside Herrmannsen’s type designation.

*croceus*, *Euplocamus* – Philippi, 1836a: ix, 103–104, pl. 7, figs. 1a–d; 1844g: 76, as *Idalia*. Palermo, Sicily, Italy. Synonym of “*Kaloplocamus*” *ramosus* (Cantraine, 1835) (Schmekel & Portmann, 1982: 109–110, pl. 6, fig. 4; text-fig. 7.38; Sabelli et al., 1990: 252).

*frondosus*, *Euplocamus* – Philippi, 1839a: 114–115. Neapolitan Sea. Synonym of “*Kaloplocamus*” *ramosus* (Cantraine, 1835) (Schmekel & Portmann, 1982: 109–110, pl. 6, fig. 4; text-fig. 7.38; Sabelli et al., 1990: 252, as “1836”).

#### Arminidae

*pustulosa*, *Diphyllidia* – Philippi, 1836a: ix, 106, ex Schultz ms; 1844g: 82, 300, pl. 19, fig. 12a–c. Palermo, Sicily, Italy. Synonym of *Armina maculata* Rafinesque, 1814 (Schmekel & Portmann, 1982: 173–174; Sabelli et al., 1990: 262; Kolb, 1998: 364).

#### Tritoniidae

*quadrilatera*, *Tritonia* – Philippi, 1836a: ix, 103, ex Schultz ms; 1844g: 75, 300, pl. 19, fig. 2. Palermo, Sicily, Italy. Synonym of *Marionia blainvillea* (Risso, 1818) (Schmekel & Portmann, 1982: 148–149, pl. 6, fig. 4; text-fig. 7.38; Cattaneo-Vietti et al., 1990: 142–143, pl. 9, fig. 6; Sabelli et al., 1990: 261).



## Tethyidae

"*Thetys*" – Sherborn (1931: 6490) attributed this error for *Tethys* Linnaeus, 1767, to Philippi (1836a: ix, 103; 1844g: 75). However, Férussac (1821: xxviii) was the first to use this misspelling (Pilsbry, 1895d: 349).

## Aeolidiidae

*limacina*, *Eolis* – Philippi, 1844g: 73–74, 300, pl. 19, fig. 1, 1a–c. Palermo, Sicily, Italy. *Aeolidiella* sp. (T. Gosliner & Á. Valdes, pers. commun., June 2013).

## Facelinidae

*scacchiana*, *Eolis* – Philippi, 1844g: 74, 300, pl. 19, fig. 6. Naples; Scacchi. *Facelina* sp. (T. Gosliner & Á. Valdes, pers. commun., June 2013).

## PULMONATA

## Siphonariidae

*laevis*, *Siphonaria* – Philippi, 1846h: 51. Chile. Synonym of the Chilean *Siphonaria lessoni* Blainville, 1824 (Rios, 1994: 223, pl. 77, fig. 1101; Forcelli, 2000: 132), or a *nomen dubium* (Güller et al., 2016: 86).

*lecanium*, *Siphonaria* – Philippi, 1846h: 51. Mazatlán, Sinaloa, Mexico. Synonym of *Siphonaria maura* G. B. Sowerby I, 1835 (Dall, 1909: 290; Keen, 1974: 852, fig. 2422). *Siphonaria "lecania"* (Strong & Hanna, 1930: 21) is an unjustified emendation (White & Dayrat, 2012: 64).

*magellanica*, *Siphonaria* – Philippi, 1855a: 208–209; 1856c: 100; 1856e: 165–166. Strait of Magellan, Chile. Syntypes, SMF 302791 (17.9 mm x 13.8 mm x 9.6 mm); MNHNS (n = 6). Synonym of *Siphonaria lessoni* Blainville, 1827 (Güller et al., 2016: 83, 86 figs. 1C, 1D, syntypes).

*tenuis*, *Siphonaria* – Philippi, 1860a: 181–182 [1860b: 163, Zool. pl. 7, fig. 5, not cited in text]. Mouth of Río Bueno, south of Isla Blanca, Chile. Synonym of *Siphonaria lessoni* Blainville, 1824 (Rios, 1994: 223, pl. 77, fig. 1101), or a valid species (Ramírez et al., 2003: 265); further study is required (Güller et al., 2016: 86, 93).

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"*savignyi*, *Siphonaria*" – Krauss (1848: 61) attributed this name to Philippi, but Krauss was

the first to describe it (Bouchet & Danrigal, 1982: 15; syntypes in MNHN Paris).

## Chilinidae

*angusta*, *Chilina* – Philippi, 1860a: 185 [1860b: 166], Zool. pl. 7, fig. 14. Quellen [springs], Atacama coast, Chile. Syntypes, SMF 302759 (n = 3) (largest, 16.4 mm x 8.9 mm). *Chilina angusta* Philippi, 1860 (Stuardo, 1961: 19; Valdovinos, 1999: 146; Letelier et al., 2003: 95).

## Lymnaeidae

*flavus*, *Limnaeus* – Philippi, 1851c: 78. Liew-Kiew Island [Ryukyu Islands, Japan]; Cécille via Largilliert.

*sandwicensis*, *Limnaeus* – Philippi, 1845i: 63. Oahu, Hawaii. Syntypes, NHMUK 1950.5.16.2-5 (n = 4) (ex Cuming); SMF 303540 (n = 4). Synonym of *Lymnaea rubella* Lea, 1841 (Cowie et al., 1995: 33).

*solidus*, *Limnaeus* – Philippi, 1844g: 121, 301, 301, pl. 21, fig. 5, in pl. expl. as "*L. gibilmannicus solidus*". Gibilmanna, northern Sicily, Italy. Syntypes, SMF 303441 (n = 3) (largest, 12.3 mm x 8.3 mm); ZMB 109752 (n = 2) (largest, 12.5 mm x 8.2 mm). Synonym of *Lymnaea peregra* (O. F. Müller, 1774) (Hubendick, 1951: 203).

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"*labiosus*, *Limnaeus*" – Clessin (in Küster, Dunker & Clessin, 1886: 397, pl. 16, figs. 3–4) described this species using a Philippi manuscript name.

"*turritus*, *Limnaeus*" – Baker (1945: 354) listed "*Limnaeus turritus* Philippi in coll. Dunker (vide Martens)" in the synonymy of *Galba attenuata* (Say), but no one made this manuscript name available (Hubendick, 1951: 206, listed as a *nomen nudum*).

"*volutata*, *Limnaea*" – Sykes (1900: 406), in his bibliographic citation for Philippi (1845i), erroneously stated that *Lymnaea volutata* Gould, 1848, was described by Philippi in 1845; this was a lapsus for *L. sandwicensis*.

## Planorbidae

*foncki*, *Ancylus* – Philippi, 1866a: 38–39. Llanquihue, Chile; Fr. Fonck. *Ancylus fonckii* Philippi, 1866 (Biese, 1949: 233–234, fig. 10; Stuardo, 1961: 26), or as *Uncancylus fonckii* (Philippi, 1866) (Santos, 2003: 214–215, fig. 57; Letelier et al., 2003: 100).



*lauricochae*, *Planorbis* – Philippi, 1869a: 38. Laguna Lauricocha & Río Maraño, Amazonas, Peru. *Biomphalaria lauricochae* (Philippi, 1869) (Ramírez et al., 2003: 272).

*raimondi*, *Planorbis* – Philippi, 1869a: 38–39. “Pampa del Sacramento” River, Peru. As “*raymondī*” in error (Clessin, 1886: 414, plate caption, *non* Bourguignat, 1864). As *Planorbis* “*incertae sedis*” (Harry, 1962: 47).

*rivularis*, *Physa* – Philippi, 1836a: xi, 146, pl. 9, fig. 1. Siracusa, Sicily, Italy, in streams. *Bulinus (Isidora) truncatus rivularis* (Philippi 1836) (Falkner et al., 2001: 28).

*subangulatus*, *Planorbis* – Philippi, 1844g: 119–120, 301, pl. 21, fig. 6, *non* Lamarck, 1807. Palermo, Sicily, & Liguria, Italy. Syntypes, SMF 303735 (n = 4). *Planorbis philippianus* Monterosato, in Caziot, 1902, is a replacement name, but is itself a junior homonym of *P. philippianus* Dunker, 1848 (described from Bolivia); *P. philippii* Germain, 1908, is the next available replacement name. Some authors (Bacci, 1940: 457; Brown, 1965: 67) listed “*Planorbis planorbis philippii* Monterosato” (from Egypt) which appears to be a misspelling of “*philippianus*” and not a senior homonym of Germain’s name. *Planorbis philippii* (Germain 1908) (Kantor & Sysoev, 2005: 221, as “*philippianus*”).

*trigyrus*, *Planorbis* – Philippi, 1869a: 39. Pimentel, Peru. *Tropicorbis (Lateorbis) trigyrus* (Philippi, 1869) (Baker, 1945: 85), or *Biomphalaria trigyra* (Philippi, 1869) (Ramírez et al., 2003: 272).

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“*bolivianus*, *Planorbis*” – Dunker (in Küster, Dunker & Clessin, 1850: 60–61, pl. 10, figs. 35–37) described this species using a Philippi manuscript name. Clessin (1886: 408, pl. 16, figs. 10–12) erroneously attributed this species to Philippi alone. Harry (1962: 42) referred this species to the “group of *Taphius glabratus* (Say, 1818).”

“*intermedius*, *Planorbis*” – Dunker (in Küster, Dunker & Clessin, 1850: 39) listed this name as a Philippi taxon, and published it in synonymy of *Planorbis tumidus* Pfeiffer, 1839 (from Cuba). Dunker cited “Philippi Conch. Cab. I Taf. I 17.16 Fig. 18.19”, which is actually plate 16, figs. 18–19 of the same volume (published by Küster in 1844, but without caption). Clessin (in Küster, Dunker & Clessin, 1884: 196, pl. 11, figs. 1–2, pl. 16, figs. 18–19), in the same volume, instead treated this name as a valid species from Veracruz, Mexico and provided a description, thereby

making the name available, albeit as a junior homonym of *P. intermedius* Charpentier, 1837 (Harry, 1962: 37). However, there is no indication that Philippi ever described “*intermedius*.”

“*largillierti*, *Segmentina*” – Pilsbry & Ferriss (1906: 166) attributed this species to “Philippi” and made it the type species of the new subgenus *Polypylis* Pilsbry, 1906. However, this species was first described by Martens, 1867 ex Dunker ms. Baker initially listed this correctly as a Dunker species, but later in the same publication attributed it to Philippi, and misspelled the name as “*largilliarti*” (Baker, 1945: 104, 394).

“*liebmanni*, *Planorbis*” – Thompson (2011: 69) attributed this species to “Philippi, 1850; in Dunker, Martini & Chemnitz, Syst. Conch. Cab., 17: 59; pl. 10, figs. 32–34”, but the authorship of that section is by Dunker (1850: 59), who made no mention of Philippi in connection with this species. Baker (1945: 48, 80) and Harry (1962: 35) correctly attributed this species to Dunker.

“*merguiensis*, *Planorbis*” – Clessin (in Küster, Dunker & Clessin, 1884: 140, pl. 12, figs. 26–28, pl. 20, fig. 4) attributed this name to Philippi, but it was first described by Hanley & Theobald (1876: 60, pl. 151, figs. 5–6), who wrote that “our specimens were received from Philippi thus named, but we cannot find where he has described them.” *Indoplanorbis exustus* (Deshayes, 1834) (Brandt, 1974: 234–235, 376, pl. 16, fig. 89; Coan & Kabat, 2012: 337).

“*paulsoni*, *Ancylus*” – Biese (1949: 232–233) listed this Philippi manuscript name, which he described as *Ancylus gayanus* var. *rudolfii*, from Quillota, Chile.

“*pulchellus*, *Planorbis*” – Clessin (in Küster, Dunker & Clessin, 1884: 137–138, pl. 11, fig. 6, pl. 16, figs. 12–14) described this species using a Philippi manuscript name, from Bolivia. Harry (1962: 40) listed this species in the “Group of *Drepanotrema kermatoides*” (d’Orbigny, 1835).

“*silesiacus*, *Planorbis*” – Clessin (in Küster, Dunker & Clessin, 1882: 89–90; 1886: 408) listed this Philippi manuscript name in the synonymy of *Planorbis dazuri* Mörch, 1868, and explained that Dunker had originally identified the specimens in pl. 14, figs. 32–35 as “*silesiacus*” but they were merely juveniles of Mörch’s species.

“*tenuis*, *Planorbis*” – Dunker (in Küster, Dunker & Clessin, 1850: 45–46, pl. 9, figs. 14–19) described this species from a Philippi manu-



script name, and cited "Philippi Conch. Cab. Taf. I 17.16 Fig. 23.24.25" which is actually plate 16, figs. 23–25 of the same volume (published by Küster in 1844, but without caption), as noted by Clessin in the "Nachträge" (errata) at the end of this volume (Clessin, 1886: 407). Clessin (1886: 407, pl. 16, figs. 23–25) erroneously attributed this species to Philippi alone. As "*Helisoma tenue* (Philippi)" in Baker (1945: 149, 430).

"*valdivianus*, *Ancylus*" – Biese (1949: 234–235, fig. 11) listed this Philippi manuscript name, which he described as *Ancylus philippianus*, from Río Cruces, Valdivia, Chile. *Hebetancylus philippianus* (Biese, 1949) (Santos, 2003: 212).

### Physidae

*mexicana*, *Physa* – Philippi, 1841: 5–6; 1843: pl. 1, figs. 3, 4, in: Küster, Dunker & Clessin, 1841–1886. Mexico. Block of text signed at bottom by Philippi. *Haitia mexicana* (Philippi, 1841) (Taylor, 2003: 140–146, 231, figs. 136–139, pl. 7, figs. 1–15; Thompson, 2011: 78–79).

*nitens*, *Physa* – Philippi, 1841: 5; 1843: pl. 1, figs. 1, 2, in: Küster, Dunker & Clessin, 1841–1886. Mexico. Block of text signed at bottom by Philippi. Possible syntypes, ZMB 121034 (larger, 23.2 mm x 11.9 mm). *Mexinauta nitens* (Philippi, 1841); type species (OD) of *Mexinauta* Taylor, 2003 (Taylor, 2003: 74–75, 82–85, 234, figs. 58–65, pl. 1, figs. 5–7, fig. 53; Thompson, 2011: 76).

*solida*, *Physa* – Philippi, 1841: 6–7; 1843: pl. 1, fig. 5, in Küster, Dunker & Clessin, 1841–1886. New Orleans, Louisiana. Block of text signed at bottom by Philippi. Probable synonym of *Haitia mexicana* (Philippi, 1841) (Taylor, 2003: 243–244).

### Ellobiidae

*Laemodonta* – Philippi, 1846i: 98, ex H. Adams ms. Type species (M): *Auricula striata* Philippi, 1846. Recent, Hawaii. Frias Martins (1996: 204–205) determined that this is a valid genus and discussed its complex nomenclatural history. Philippi's type species is a junior homonym; *Pedipes octanfracta* Jonas, 1845, is the earliest available name.

*botteriana*, *Auricula* – Philippi, 1846i: 97. Lesina, Dalmatia [Hvar, Croatia]; Botteri. Synonym of *Ovatella myosotis* (Draparnaud, 1801) (Frias Martins, 1996: 194–195, 202; Kantor & Sysoev, 2005: 227–228).

*bronnii*, *Auricula* – Philippi, 1846i: 98. Hawaii; Bronn. The Hawaiian endemic *Allochroa bronnii* (Philippi, 1846) (Kay, 1979: 491–492, fig. 157F, G; Frias Martins, 1995: 3–5); type species (OD) of *Allochroa* Ancey, 1887.

*cecillii*, *Scarabus* – Philippi, 1847r: 122–123. China; Largilliert. *Pythia cecillii* (Philippi, 1847) (Higo et al., 1999: 404; Okutani, 2000: 816–817, fig. 3, as "*cecillei*"; Qi, 2004: 197, pl. 108B, as "*cecillei*" and "1848").

*hepatica*, *Auricula* – Philippi, 1851b: 54. Liew-Kiew Island, China [Ryukyu Islands, Japan]; Cécille via Largilliert.

*striata*, *Auricula* – Philippi, 1846i: 98, ex H. Adams ms, *non A. striata* Martens, 1824, *non* Anton, 1839. Hawaii. Synonym of *Laemodonta octanfracta* (Jonas, 1845) (Kay, 1979: 491–492, fig. 157B; Higo et al., 1999: 405; Severns, 2011: 426–427, pl. 194, fig. 3).

*triticea*, *Auricula* – Philippi, 1845i: 63. "China?" Attributed by Sherborn (1924: 6636) to "Philippi in Küster (1841)," but not published by Küster until 1845 (pp. 49–50). Because Philippi's publication can be dated to September 1845, while Küster (1845) has no specific month, Philippi's description has precedence over that of Küster.

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"*bivonae*, *Auricula*" Sherborn (1924: 801) attributed this species to "Philippi" in Küster (1841: 20–21, pl. 1, figs. 14–15). However, this species was indicated by Küster to be "in litt." and the text appears to be entirely by Küster, based on information communicated ("mitgetheilt") by Philippi, so we consider that this species should be attributed to "Küster, ex Philippi ms". Sabelli et al. (1990: 271) also listed this as a "Philippi" name, in the synonymy of *Auriculinella erosa* (Jeffreys, 1830).

"*fusca*, *Auricula*" Sherborn (1926: 2599) attributed this species to "Philippi" in Küster (1844: 38–39, pl. 5, figs. 18–20). However, as for the previous entry, this species should be attributed to "Küster, ex Philippi ms".

"*nigra*, *Auricula*" Sherborn (1928: 4310) attributed this species to "Philippi" in Küster (1841: 23, pl. 3, figs. 4–5). However, as for the previous two entries, this species should be attributed to "Küster, ex Philippi ms".

### Onchidiidae

*nanum*, *Onchidium* – Philippi, 1841a: 56–57, 59, pl. 5, fig. 8; 1844g: 101, 301, pl. 20, fig.



6, 6a. Palermo, Sicily, Italy. *Onchidella nana* (Philippi, 1844) (Falkner et al., 2001: 30).

#### Succineidae

*aprica*, *Succinea* – Philippi, 1858b: 22. San Juan, Concepción, Chile.

*fernandeziana*, *Succinea* – Philippi, 1858b: 22. Isla Juan Fernandez, Chile.

*labiosa*, *Succinea* – Philippi, 1860a: 182 [1860b: 164], Zool. pl. 7, fig. 7. Tilopozo, Chile. *Succinea labiosa* Philippi, 1860, from Atacama and northern Argentina (Stuardo & Vega, 1985: 128; Valdovinos, 1999: 148; Letelier et al., 2003: 102).

*peruviana*, *Succinea* – Philippi, in Pfeiffer, 1867a: 78–79. Peru. *Succinea peruviana* Philippi in Pfeiffer, 1867 (Crawford, 1939: 321; Ramírez et al., 2003: 276).

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“*chiloensis*, *Succinea*” – “Philippi, in Pfeiffer”, 1848: 527–528. This species was listed as by Philippi in Pfeiffer in Sherborn (1925: 1232), but Pfeiffer noted that it was a ms. name, and there is no evidence that Philippi was responsible for its description.

#### Pupillidae

*bryophila*, *Helix* – Philippi, 1855b: 216–217; 1856b: 93; 1856d: 156. Canelos, Valdivia, Chile. As *Helix* (Tryon, 1887b: 42, pl. 9, figs. 79–80); Endodontidae (Stuardo & Vega, 1985: 130); now in Pupillidae (Breure, pers. comm. 2013).

*coiguecana*, *Helix* [as “*Golix*”] – Philippi, 1855b: 216; 1856d: 155–156. Valdivia, Chile. Endodontidae (Stuardo & Vega, 1985: 130); now in Pupillidae (Breure, pers. comm. 2013).

*corticaria*, *Helix* – Philippi, 1855b: 216; 1856b: 92; 1856d: 155. Near Río Coigueco, Valdivia, Chile. Endodontidae (Stuardo & Vega, 1985: 130); now in Pupillidae (Breure, pers. comm. 2013).

*exigua*, *Helix* – Philippi, 1855b: 217; 1856b: 93; 1856d: 156–157, *non* Stimpson, 1850 (eastern North American species now placed in genus *Striatura*) (B. Roth, in litt., 29 Dec. 2014). Valdivia, Chile. Endodontidae (Stuardo & Vega, 1985: 130); now in Pupillidae (Breure, pers. comm. 2013). However, as Philippi’s species name is a junior homonym, it would require renaming in order to be used.

*germaini*, *Helix* – Philippi, 1855b: 214–215; 1856b: 91; 1856d: 154. Mountains near

Pirque, Santiago, Chile. Endodontidae (Stuardo & Vega, 1985: 130); now in Pupillidae (Breure, pers. comm. 2013).

*hypophloea*, *Helix* – Philippi, 1855b: 215–216; 1856b: 92; 1856d: 155. Near Río Coigueco, Valdivia, Chile. Endodontidae (Stuardo & Vega, 1985: 130); now in Pupillidae (Breure, pers. comm. 2013).

*jungermanniarum*, *Helix* – Philippi, 1855b: 217; 1856b: 91; 1856d: 154. Valdivia, Chile. Endodontidae (Stuardo & Vega, 1985: 130); now in Pupillidae (Breure, pers. comm. 2013).

*limensis*, *Pupa* – Philippi, 1867a: 75–76. San Bartolomeo, near Lima, Peru. *Pupoides* (*Ischnopupoides*) *limensis* (Philippi, 1867) (Stuardo & Vargas Almonacid, 2000), or a junior synonym of *Pupoides paradesii* (d’Orbigny, 1835) (Ramírez et al., 2003: 274).

*minimus*, *Bulimus* – Philippi, 1860a: 184–185 [1860b: 166], Zool. pl. 7, fig. 12. Cachinal & Paposo, Chile. Haas (1956: 84) transferred this species from the Bulimulidae to the Vertiginidae, as *Pupoides* (*Ischnopupoides*) *minimus* (Philippi, 1860); Biese (1960: 133–135, pl. 13, figs. 1–4), Stuardo & Vega (1985: 127), Valdovinos (1999: 147), Stuardo & Vargas Almonacid (2000), Letelier et al. (2003: 101) and Araya & Catalán (2014: 42), all listed this taxon in the Pupillidae.

*minviellei*, *Helix* – Philippi, in Pfeiffer, 1867a: 80, unnecessary new name for *Helix pazi* Philippi, 1866a, which is not preoccupied by *Helix pazensis* Poey, 1854. An incorrect spelling based on Patricio Paz y Membiela (1808–1874), which Philippi and Pfeiffer misspelled as “Patricio Paz Minvielle” (Hidalgo, 1872: 31).

*musculicola*, *Helix* – Philippi, 1855b: 216; 1856b: 92–93; 1856d: 156. Canelos, Valdivia, Chile. Endodontidae (Stuardo & Vega, 1985: 130); now in Pupillidae (Breure, pers. comm. 2013).

*pazi*, *Helix* – Philippi, 1866a: 39. Valparaíso, Chile; Patricio Paz-Minvielle [Patricio Paz y Membiela, Comisión Científica del Pacífico]. Unnecessarily renamed *Helix minviellei* Philippi, 1867 (*supra*). Endodontidae (Stuardo & Vega, 1985: 130); now in Pupillidae (Breure, pers. comm. 2013).

*tenuistria*, *Helix* – Philippi, 1855b: 215; 1856b: 92; 1856d: 154–155. Mountains near Pirque, Santiago, Chile. *Amphidoxa tenuistriata* (Philippi, 1855) (Pilsbry, 1895b: 340); or Endodontidae (Stuardo & Vega, 1985: 130); now in Pupillidae (Breure, pers. comm. 2013).



## Chondrinidae

*rupestris*, *Bulimus* – Philippi, 1836a: xi, 141, pl. 8, fig. 18 [as “15” in error in text], *non* Krynicki, 1833; 1844g: 113–114, as *Pupa*. Palermo & Sciacca, Sicily, Italy. Lectotype, ZMB 9653 (Palermo), designated by Beckmann (2002: 58, pl. 10, fig. 1); 4 paralectotypes ZMB 9653b; 4 paralectotypes NHM Wien (Palermo); 6 paralectotypes SMF 54440; 2 paralectotypes SMF 246256. *Rupestrella rupestris* (Philippi, 1836) (Beckmann, 2002: 58–60, pl. 10, figs. 1–8, pl. 11, fig. 11). Type species (OD) of *Rupestrella* Monterosato, 1894. A petition was submitted to the ICZN to conserve Philippi’s name, since Krynicki’s name is now in classified in *Peristoma*, in a different family, the Enidae (Balashov & Welter-Schultes, 2015).

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“*caprearum*, *Pupa*” – Rossmässler, 1842 (June), ex Philippi ms: 11, pl. 53, fig. 729. Naples. Although listed by Sherborn (1924: 1068) as “Philippi in Rossmässler”, Rossmässler clearly indicated that this was a Philippi manuscript name. *Granopupa philippi* (Cantraine, 1841) (Pilsbry, 1918a: 342).

“*pallida*, *Pupa*” – Rossmässler, 1842 (June), ex Philippi ms: 11–12, pl. 53, fig. 732. Upper Italy. Although listed by Sherborn (1929: 4705) as “Philippi in Rossmässler”, Rossmässler clearly indicated that this was a Philippi manuscript name. *Chondrina pallida* (Rössmassler, 1842) (Pilsbry, 1918b: 63).

## Vertiginidae

*schultzii*, *Pupa* (?*Vertigo*) – Philippi, 1844n: 106. Palermo, Sicily, Italy; Schultz. *Vertigo schultzii* (Philippi, 1844) (Pilsbry, 1919: 202, pl. 18, fig. 9).

## Enidae

*cantorii*, *Bulimus* – Philippi, 1844z: 165. Auri Island, Nang-king, China; [Largilliert]. Type species (M) of *Mirus* Albers, 1850. *Mirus cantorii* (Philippi, 1844) (Yen, 1939: 78, pl. 7, fig. 1; 1942: 252, as “*cantor*” which is in error, ICZN Code Art. 31.1.3 (1999)).

*dardanus*, *Bulimus* – Philippi, 1844u: 158 [8], pl. 2, fig. 5, ex Frivaldsky ms. Constantinopolis, Turkey. The description was signed by Philippi. *Zebrina dardana* (Philippi, 1844) (Heller, 1976: 374).

*loewii*, *Bulimus* – Philippi, 1844n: 106, footnote. Asia Minor (“Rhodus?”). *Jaminia loewii* (Philippi 1844), from Turkey (Heller, 1976: 378).

## Clausiliidae

*affinis*, *Clausilia* – Philippi, 1836a: xi, 139. Sicily, Italy. Syntype, ZMB 12281 (14.5 mm x 3.1 mm). *Papillifera bidens* var. *affinis* (Philippi, 1836) (Falkner et al., 2001: 40; Nordsieck, 2007: 54, 2013: 8).

*calcarae*, *Clausilia* – Philippi, 1844n: 107. Palermo. *Charpentieria (Siciliaria) calcarae* (Philippi 1844) (Nordsieck, 2002: 29; 2007: 53).

*cecillii*, *Clausilia* – Philippi, in Pfeiffer, 1847: 68. China; Largilliert. Possible syntypes, NHMUK 196606 (n = 3) (30.4 mm x 6.5 mm; 29.0 mm x 6.6 mm; 28.3 mm x 6.5 mm). Boettger & Schmacker (1894: 115), Yen (1942: 258) and Nordsieck (1998: 129) cited these syntypes. *Hemiphaedusa cecillei* (Philippi, in Pfeiffer, 1847) (Yen, 1939: 94, pl. 9, figs. 12–13; 1942: 258). Nordsieck (1998: 129) incorrectly attributed authorship of this species to Pfeiffer alone.

*cinerea*, *Clausilia* – Philippi, 1836a: xi, 145, pl. 8, fig. 24; 1844g: 115. Castellamare Naples, & Salerno, Italy. Syntypes SMF 137107 (n = 3); SMF 137108 (n = 1). Synonym of *Leucostigma candidescens* (Rossmässler, 1835), or a subspecies thereof (Zilch, 1977: 143, pl. 10, fig. 43).

*cornea*, *Clausilia* – Philippi, in Pfeiffer, 1846: 63; Philippi, in Küster, 1844: pl. 2, figs. 1–4; Philippi, in Küster, 1847: 22–23. Java; Junghuhn. The uncaptioned plate (1844) appeared two years before a caption appeared in Pfeiffer’s *Symbolae* (1846), and three years before the text in Küster (1847) appeared. We consider that Philippi is both responsible for the name in Pfeiffer (1846) and for its eventual description in Küster (1847). This taxon is the type species (SD Kennard & Woodward, 1923) of *Acrophaedusa* Boettger, 1877.

*junghuhnii*, *Clausilia* – Philippi, in Pfeiffer, 1846: 63; Philippi, in Küster, 1844: pl. 2, figs. 5–7; Philippi, in Küster, 1847: 23–24. Java; Junghuhn. The uncaptioned plate (1844) appeared two years before a caption appeared in Pfeiffer’s *Symbolae* (1846), and three years before the text in Küster appeared. We consider that Philippi is both responsible for the name in Pfeiffer (1846) and for its eventual description in Küster (1847).



- largillierti*, *Clausilia* – Philippi, in Pfeiffer, 1847: 68. China; Largilliert. Syntypes, Muséum de Rouen 201401600 (n = 17, largest 32.2 mm x 7.9 mm); SMF 304504 (n = 2) (larger, 28.4 mm x 6.9 mm). *Hemiphaedusa pluvialis* (Benson, 1842) (Nordsieck, 1998: 128; 2007: 28).
- malleolata*, *Clausilia* – Philippi, 1867b: 194, pl. 2, figs. 3, 4. Between Contumaza and Cajamarca, Peruvian Andes. *Steeriana* (S.) *malleolata* (Philippi, 1867) (Loosjes & Loosjes-van Bemmelen, 1984: 37, fig. 11; Abbott, 1989: 67; Ramírez et al., 2003: 275; Nordsieck, 2007: 42, pl. 9, fig. 6).
- paestana*, *Clausilia* – Philippi, 1836a (pre-April): 138–139, footnote, 145; Rossmässler, 1836 (March or later): 13, pl. 12, fig. 172, ex Philippi ms; Philippi, 1844g: 116. Pasti, Sicily; in ruins. Lectotype, SMF 312488, designated by Nordsieck (2002: 31, 35, fig. 6); paralectotypes, ZMB 9863 (n = 3), SMF 304482. *Charpentieria* (*Stigmatica*) *paestana* (Philippi, 1836) (Nordsieck, 2002: 31, 35), or as *Sicilaria* (*Stigmatica*) *paestana* (Philippi, 1836) (Nordsieck, 2013: 7). Type species (T) of *Paestana* Westerlund, 1884, now considered to be a synonym of *Sicilaria* Vest, 1867.
- peruviana*, *Balea* – Philippi, in Pfeiffer, 1867a: 78. Yanaoca, Cuzcoensis, Peru. Type species (M) of *Exbalea* Jousseame, 1900. Synonym of *Temesa clausilioides* (Reeve, 1849) (Sykes, 1901: 220–221, fig. 1), or *T. peruviana* (Philippi, in Pfeiffer, 1867) (Crawford, 1939: 322–323, pl. 19, fig. 14, attributed to Pfeiffer).
- raimondii*, *Clausilia* – Philippi, 1867b: 195, pl. 2, figs. 5–7. Between San Gregorio and Patipampa “ad orientem oppidi Huancayo”, Peru; Ant. Raimondi. Lectotype, MHNL 0025H (Museo de Historia Natural, Lima) (16.2 mm x 3.0 mm), designated by Loosjes & Loosjes-van Bemmelen (1989: 89, fig. 5); paralectotypes SMF 135519 (n = 5) (Zilch, 1954: 66, pl. 5, figs. 2–3). Type species (OD) of *Gibbonenia* Zilch, 1954. *Gibbonenia raimondii* (Philippi, 1867) (Loosjes & Loosjes-van Bemmelen, 1989: 87–89, fig. 5; Ramírez et al., 2003: 275; Nordsieck, 2007: 41).
- sarsii*, *Balea* – Philippi, in Pfeiffer, 1847: 84. Norway; Sars. Proschwitz (2010: 17–18) discussed this species from Norway and determined that *B. heydeni* Maltzan, 1881, is a junior synonym. Welter-Schultes et al. (2011: 18, 20) erroneously attributed this name to “Menke & Pfeiffer,” referring to the editors of the journal. However, this article

is by Pfeiffer, and this species name is by Philippi. Bank (2011: 18) and Welter-Schultes & Audibert (2013: 17) attributed this name to “Pfeiffer, 1847”, but we conclude that since Philippi contributed the species description, it should be “Philippi, in Pfeiffer, 1847.”

*semplicata*, *Clausilia* – Philippi, 1836a: xi, 139, 256, pl. 8, fig. 22, 22a; 1844g: 116. Palermo, Sicily, Italy. Syntypes, SMF 304531 (n = 1) (17.9 mm x 4.8 mm); ZMB 9886 (19.3 mm x 4.5 mm; 17.4 mm x 3.5 mm). *Charpentieria* (*Sicilaria*) *semplicata* (Philippi, 1836) (Nordsieck, 2002: 29; 2007: 54, pl. 13, fig. 7).

*syracusana*, *Clausilia* – Philippi, 1836a (pre-April): 139, 256, pl. 8, fig. 23; Rossmässler, 1836 (Sept. or later): 13–14, pl. 18, fig. 255, ex Philippi ms. Siracusa, Sicily, Italy. Lectotype, RMNH 55916 (Malta), designated by Beckmann & Gittenberger (1987: 336, pl. 29, fig. 1); paralectotypes SMF 67137 (labeled as “holotype”), SMF 67318, and ZMB 9801. *Muticaria syracusana* (Philippi, 1836) (Nordsieck, 2007: 49, pl. 12, fig. 3).

#### Orthalicidae *sensu lato*

Breure & Romero (2012) have recently concluded that the Bulimulidae, Odontostomidae, Simpulopsidae and Amphibuliminae (treated as subfamilies of the Orthalicidae by Bouchet & Rocroi, 2005: 266), should each be elevated to a full family. However, as not all of Philippi’s species of “*Bulimus*” have been allocated to a modern family, and the family-level classification of this group may change with further study, we have retained the broader use of “Orthalicidae” with Megaspiridae used for several species of “*Bulimus*” that are now placed in *Thaumastus*.

*alsophilus*, *Bulimus* – Philippi, 1867a: 69–70; Pfeiffer, 1867: 334, pl. 80, figs. 3, 4. Between Lamas and Tarapoto, Peru. *Drymaeus alsophilus* (Philippi, 1867) (Ramírez et al., 2003: 279).

*arbustorum*, *Bulimus* – Philippi, 1858b: 21. Valdivia, Chile. Junior synonym of *Bulimus ochsenii* Dunker, 1855 (Pilsbry, 1897: 10, pl. 8, figs. 28–29), now *Plectostylus ochsenii* (Dunker, 1855) (Köhler, 2007: 142).

*aurisratti*, *Bulimus* – Philippi, 1867a: 69, as “*B. auris ratti*”; Pfeiffer, 1867: 336–337, pl. 80, figs. 10, 11. Between Lamas and Tarapoto, Peru. Probable holotype, SMF 156341 (Neubert & Janssen, 2004: 200, pl. 15, fig. 175). *Drymaeus aurisratti* (Philippi, 1867) (Ramírez



- et al., 2003: 279), or synonym of *Drymaeus* (D.) *expansus* (Pfeiffer, 1867) (Neubert & Janssen, 2004).
- bifasciatus*, *Bulimus* – Philippi, 1845m: 10 [10]. See under: *B. bivittatus* Philippi, 1845i.
- bivittatus*, *Bulimus* – Philippi, 1845i: 62, *non* G. B. Sowerby I, 1833; 1845m: 10–11 [10–11], pl. 3, fig. 5, as *B. bifasciatus*. Forests of Peru; E. B. Philippi. In his second account, Philippi (1845m) claimed that the original name had been a typographical error, but his original spelling ordinarily has to be used (ICZN Code Article 32 (1999)). While *B. bifasciatus* was thus an unjustified emendation, it is nonetheless an available name (ICZN Code Article 33.2.3 (1999)). *Bulimus bivittatus* Philippi, 1845, is *non* G. B. Sowerby I, 1833, and thus *B. bifasciatus* Philippi, 1845, becomes the valid name for this species. *Bulimus bitaeniatus* Nyst, 1845, *nom. nov. pro B. bivittatus* Philippi, 1845, *non* G. B. Sowerby I, 1833, is an unnecessary replacement name. Nyst's name is the type species (OD) of *Scholvienia* Strebel, 1910. *Thaumastus* (*Scholvienia*) *bifasciatus* (Philippi, 1845) (Ramírez et al., 2003: 282); note that *Thaumastus* (Megaspiridae) and *Scholvienia* (Orthalicidae) are now in different families; now as *Scholvienia bifasciatus* (Philippi, 1845) (Breure & Mogollón Avila, 2016: 65–67, figs 57c–e, 65c–f, 66). See also *B. bifasciatus unicolor* Philippi, 1869a.
- botterianus*, *Bulimus* – Philippi, 1846u: 126 [22], pl. 5, fig. 9. Lesina, Dalmatia [Hvar, Croatia]; Botteri.
- canarius*, *Bulimus* – Philippi, in Pfeiffer, 1867a: 76–77; Pfeiffer, 1867: 334–335, pl. 80, figs. 5–7. Trujillo, Peru. *Drymaeus* (D.) *canarius* (Philippi, in Pfeiffer, 1867) (Pilsbry, 1898: 282–283, pl. 48, figs. 36–38).
- chenui*, *Bulimus* – Philippi, 1867a: 72–73; Pfeiffer, 1867: 344–345, pl. 81, figs. 11, 12. Pachicamac, near Lima, Peru. *Drymaeus chenui* (Philippi, 1867) (Ramírez et al., 2003: 279).
- cygneus*, *Bulimus* – Philippi, 1867a: 68; Pfeiffer, 1867: 342–343, pl. 81, figs. 5, 6. “Lomas de Supe”, Peru. *Drymaeus cygneus* (Philippi, 1867) (Ramírez et al., 2003: 279).
- delicatulus*, *Bulimus* – Philippi, 1867a: 73–74; Pfeiffer, 1867: 335–336, pl. 80, figs. 8, 9. Hacienda de Unigambal, Peru. *Bostryx delicatulus* (Philippi, 1867) (Ramírez et al., 2003: 277).
- elatus*, *Bulimus* – Philippi, 1869a: 33–34; Pfeiffer, 1869a: 89; 1869b: 469–470, pl. 102, figs. 5, 6. Between Mayoc and Huanta [sic, Huantana], Pampa & near Pichicna, Peru. *Bostryx elatus* (Philippi, 1869) (Ramírez et al., 2003: 277; Breure & Mogollón Avila, 2010: 19).
- eurystomus*, *Bulimus* – Philippi, 1867a: 68; Pfeiffer, 1867: 343, pl. 81, figs. 7, 8. Chanchamayo, Peru. Fulton (1905: 21) determined that this species, which he misspelled as “*eurystomus*”, was a junior synonym of *Drymaeus hamadryas* (Philippi, 1867). However, Breure & Mogollón Avila (2010: 26) recognized it as a distinct species, *D. (D.) eurystomus* (Philippi, 1867) (see also Abbott, 1989: 99; Ramírez et al., 2003: 280).
- hamadryas*, *Bulimus* – Philippi, 1867a: 68–69; Pfeiffer, 1867: 341, pl. 81, figs. 1, 2. Chanchamayo, Peru. *Drymaeus hamadryas* (Philippi, 1867) (Fulton, 1905: 21; Ramírez et al., 2003: 279).
- heterogyrus*, *Bulimus* – Philippi, 1869a: 42; Pfeiffer, 1869a: 90–91. Between Sartimbamba and Chusgon, Libertad, Peru. *Neopetraeus heterogyrus* (Philippi, 1869) (Ramírez et al., 2003: 281).
- ignobilis*, *Bulimus* – Philippi, 1867a: 72; Pfeiffer, 1867: 340–341, pl. 80, figs. 21, 22. Chanchamayo, Peru. *Bostryx ignobilis* (Philippi, 1867) (Breure, 1978: 92; Ramírez et al., 2003: 278).
- iserni*, *Bulimus* – Philippi, 1867a: 75; Pfeiffer, 1867: 338–339, pl. 80, figs. 16–18. Near “La Oroya”, Peru; Johannes Isern. *Thaumastus* (*Scholvienia*) *iserni* (Philippi, 1867) (Breure, 1978: 46; Ramírez et al., 2003: 282); note that *Thaumastus* (Megaspiridae) and *Scholvienia* (Orthalicidae) are now in different families; now as *Scholvienia iserni* (Philippi, 1867) (Breure & Mogollón Avila, 2016: 69, figs. 65a–b, 67).
- lentiginosus*, *Bulimus* – Philippi, 1869a: 32–33. Between Cajamarca and Contumasa, Peru. *Drymaeus* (*Mesembrinus*) *lentiginosus* (Philippi, 1869) (Ramírez et al., 2003: 280).
- leucostictus*, *Bulimus* – Philippi, 1856a: 53; 1860a: 184 [1864b: 166]. Paposo, [Antofagasta], coastal Atacama desert, Chile. Lectotype, ZMB 114306a, designated by Köhler (2007: 132–133, fig. 27) (14.1 mm x 4.0 mm); one paralectotype, ZMB 114306b. *Peronaeus leucostictus* (Philippi, 1856) (Rehder, 1945: 105); *Bostryx leucostictus* (Philippi, 1856) (Breure, 1978: 97, figs. 144, 145; Stuardo & Vega, 1985: 134; Valdovinos, 1999: 150; Letelier et al., 2003: 106, the last as “*leocostictus*”).



- membranaceus*, *Bulimus* – Philippi, 1846u: 126 [22], pl. 5, fig. 2. Locality unknown. Pilsbry (1898: 237–238, pl. 44, figs. 90–91) stated that this was a South American *Drymaeus*, “possibly a Peruvian *Drymaeus*.”
- miliaris*, *Bulimus* – Philippi, 1867a: 74; Pfeiffer, 1867: 347, pl. 81, figs. 19–21. *Drymaeus* (*Mesembrinus*) *miliaris* (Philippi, 1867) (Breure & Eskens, 1981: 77–78; Ramírez et al., 2003: 280).
- monticola*, *Bulimus* – Philippi, 1869a: 33; Pfeiffer, 1869a: 88–89; 1869b: 470–471, pl. 102, figs. 7, 8, *non Bulimus monticola* Roth, 1856. Renamed *Bulimulus dendritoides* Pilsbry (1896: 186–187, pl. 50, figs. 60–61). Between San Fernando and Patipampa, Peru. *Bostryx dendritoides* (Pilsbry, 1896) (Ramírez et al., 2003: 277, who used Philippi’s name, not Pilsbry’s replacement).
- morbidus*, *Bulimus* – Philippi, 1867a: 70; Pfeiffer, 1867: 341–342, pl. 81, figs. 3, 4. Hacienda de Sunchobamba, near Cajamarca, Peru. *Drymaeus* (*D.*) *morbidus* (Philippi, 1867) (Breure & Eskens, 1981: 29–30; Ramírez et al., 2003: 279).
- nemorensis*, *Bulimus* – Philippi, in Pfeiffer, 1867a: 78; Pfeiffer, 1867: 345–346, pl. 81, figs. 15, 16. Punas, between Ayapata and Olachea, Peru. *Scutalus* (*Kuschelenia*) *nemorensis* (Philippi, in Pfeiffer, 1867) (Ramírez et al., 2003: 281), or synonym of *Scutalus culmineus* (d’Orbigny, 1835) (Crawford, 1939: 328).
- peliosomus*, *Bulimus* – Philippi, in Pfeiffer, 1867a: 77; Pfeiffer, 1869b: 466–467, pl. 101, figs. 22, 23. “Jocos” ? near Río Marañon [sic], Peru. Breure (1978: 109, pl. 7, figs. 4–5) noted that “three specimens in the IML [Instituto Miguel Lillo, Tucumán, Argentina] collection are ‘from the original series’ and were collected by A. Raimondi ‘entre Jocos y Río Marañon.’” If Philippi examined these specimens, they may constitute type material. *Bostryx peliosomus* (Philippi, in Pfeiffer, 1867) (Ramírez et al., 2003: 278).
- productus*, *Bulimus* – Philippi, in Pfeiffer, 1867a: 77; Pfeiffer, 1867: 353–354, pl. 82, figs. 23–25. Sierra Cotahuasi, Peru. *Bostryx productus* (Philippi, 1867) (Ramírez et al., 2003: 278).
- reentsii*, *Bulimus* – Philippi, 1851b: 30. “Mons” Chala, Peru; Reents coll. Possible syntype, ZMB 121035 (Peru, ex Reents). *Bostryx reentsii* (Philippi, 1851) (Stuardo & Valdovinos, 1986: 57; Abbott, 1989: 96; Ramírez et al., 2003: 278; Breure, 2008: 510, fig. 13).
- reentsii*, *Helix* – Philippi, 1855b: 214; 1856a: 52–53; 1856b: 90; 1856d: 152–153; 1860a: 182–183 [1860b: 164], zool. pl. 7, fig. 8, *non Bulimus reentsii* Philippi, 1851. Paposo, [Antofagasta], coastal Atacama desert, Chile. Renamed *Bulimulus* (*Bostryx*) *eremothauma* Pilsbry (1896: 129–130, pl. 44, figs. 83–86). *Bostryx* (*Platybostryx*) *eremothauma* (Pilsbry, 1896) (Stuardo & Valdovinos, 1986: 57).
- scalarioides*, *Bulimus* – Philippi, in Pfeiffer, 1867a: 77–78, *non* Reeve, 1849. Conchucos, Peru. Renamed *Peronaeus aequicostata* Rehder (1945: 106). *Bostryx aequicostata* (Rehder, 1945) (A. Breure, in litt., Sept. 19, 2013).
- serenus*, *Bulimus* – Philippi, 1867a: 72; Pfeiffer, 1867: 339–340, pl. 80, figs. 19, 20. Hacienda de Sunchobamba, Peru. *Drymaeus* (*Mesembrinus*) *serenus* (Philippi, 1867) (Ramírez et al., 2003: 280).
- splendidus*, *Bulimus* – Philippi, 1858b: 21–22. Isla Juan Fernandez, Chile.
- spretus*, *Bulimus* – Philippi, 1869a: 34–35; Pfeiffer, 1869a: 89–90; 1869b: 471–472, pl. 102, fig. 11, *non* Reeve, 1850. Between Mayoc and Huanta [Huantana], Peru. Renamed *Bulimulus raimondianus* Pilsbry (1896: 167, pl. 50, fig. 40). *Bostryx raimondianus* (Pilsbry, 1896) (Ramírez et al., 2003: 278).
- stigmaticus*, *Bulimus* – Philippi, 1867a: 74–75; Pfeiffer, 1867: 337, pl. 80, figs. 12, 13. “Hacienda de Unigambal”, Peru. *Drymaeus* (*Mesembrinus*) *stigmaticus* (Philippi, 1867) (Ramírez et al., 2003: 280).
- subeffusus*, *Bulimus* – Philippi, 1869a: 36; Pfeiffer, 1869b: 486, pl. 102, figs. 1, 2. Huanayo, near Coyllorbamba, Peru. *Drymaeus subeffusus* (Philippi, 1869) (Ramírez et al., 2003: 279).
- subroseus*, *Bulimus* – Philippi, in Pfeiffer, 1869a: 90; 1869b: 472–473, pl. 102, figs. 12, 13, figs. 14, 15, var. Between San Fernando and Patipampa, Peru. *Bostryx serotinus subroseus* (Philippi, in Pfeiffer, 1869) (Ramírez et al., 2003: 278).
- taeniatus*, *Bulimus* – Philippi, 1869a: 35; Pfeiffer, 1869b: 468–469, pl. 102, figs. 3, 4, *non* Mörch, 1850. Hacienda de Mariabal, Libertad, Peru. Renamed *Drymaeus libertadensis* Pilsbry (1898: 291, pl. 51, figs. 16, 19). *Drymaeus hepaticus libertadensis* Pilsbry, 1898 (Ramírez et al., 2003: 279).
- tapadoides*, *Bulimus* – Philippi, 1867a: 71; Pfeiffer, 1867: 338, pl. 80, figs. 14, 15. Tarma, Peru; Johannes Isern. *Stenostylus*



*tapadoides* (Philippi, 1867) (Ramírez et al., 2003: 282).

*tarmensis*, *Bulimus* – Philippi, 1867a: 70–71; Pfeiffer, 1867: 343–344, pl. 81, figs. 9, 10. La Oroya, Tarma, Peru. *Thaumastus tarmensis* (Philippi, 1867), from Arequipa, Peru (Grensted, 1930: 54; Ramírez et al., 2003: 282), or a synonym of *Scholvienia alutacea* (Reeve, 1850) (Breure & Mogollón Avila, 2016: 64–65).

*troscheli*, *Bulimus* – Philippi, 1867a: 71; Pfeiffer, 1867: 345, pl. 81, figs. 13, 14. Hacienda de Unigambal, Peru; 3,200 m. *Scutalus (Sunellus) troscheli* (Philippi, 1867) (Breure, 1978: 190, pl. 11, fig. 4; Ramírez et al., 2003: 281).

*trujillensis*, *Bulimus* – Philippi, 1867a: 73; Pfeiffer, 1867: 333, pl. 80, figs. 1, 2. Trujillo, Peru. *Drymaeus trujillensis* (Philippi, 1867) (Ramírez et al., 2003: 280; Breure & Ablett, 2014: 105).

*ulloae*, *Bulimus* – Philippi, 1869a: 34; Pfeiffer, 1869b: 471, pl. 102, figs. 9, 10. Between Mayoc and Huanta [Huantana], Peru. *Bulimulus ulloae* (Philippi, 1869) (Pilsbry, 1896: 167, pl. 50, fig. 41), or as “*Bulimus*” *ulloae* Philippi, 1869, *incertae sedis* (Ramírez et al., 2003: 282).

*unicolor*, *Bulimus bifasciatus* – Philippi, 1869a: 36. Hacienda de Huaribamba, east of Huancayo, Peru; Raimondi. *Thaumastus (Scholvienia) bifasciatus unicolor* (Philippi, 1869) (Ramírez et al., 2003: 282); note that *Thaumastus* (Megaspiridae) and *Scholvienia* (Orthalicidae) are now in different families; now as a junior synonym of *Scholvienia brephoides* (d’Orbigny, 1835) (Breure & Mogollón Avila, 2016: 67).

#### Megaspiridae

*crenellus*, *Bulimus* – Philippi, 1867a: 67–68; Pfeiffer, 1867: 346–347, pl. 81, figs. 17, 18. Hacienda de Unigambal, Peru. *Thaumastus (Paeniscutalus) crenellus* (Philippi, 1867) (Breure, 1978: 34–37, figs. 37–41; Ramírez et al., 2003: 282; Breure & Mogollón Avila, 2010: 16–17); *Paeniscutalus crenellus* (Philippi, 1867) (Breure & Mogollón Avila, 2016: 26, figs. 17–18).

*largillierti*, *Bulimus* – Philippi, 1845m: 11 [11], pl. 3, fig. 6. Santa Catarina [state], Brazil; Largilliert. Probable syntype, ZMB 112728 (50.4 mm x 21.4 mm) (Köhler, 2007: 129, 131, fig. 17). *Thaumastus largillierti* (Philippi, 1845) (Simone, 2006: 153, fig. 520; Breure

& Ablett, 2015: 26; Breure & Mogollón Avila, 2016: 25).

#### Urocoptidae

*binneyana*, *Cylindrella (Pupa)* – Philippi, 1845t: 49 [10], pl. 2, figs. 11, 17, ex [H.] Adams ms. Jamaica. It seems likely from the following species in this publication, where the “H.” is present, that Henry Adams was also the source of the name. Pilsbry (1902b: 141) erroneously listed this as a junior synonym of *Urocoptis nobilior* (C. B. Adams, 1848), but Philippi’s name has precedence by three years.

*pallida*, *Cylindrella (Brachypus)* – Philippi, 1845t: 52 [13], pl. 2, fig. 14, ex Guilding ms. “India Occidentali”. *Brachypodella pallida* (Philippi, 1845), from the Caribbean (Pilsbry, 1903b: 84–85, pl. 7, figs. 30–31).

*seminuda*, *Cylindrella* – Philippi, 1845t: 51 [12], pl. 2, fig. 16, ex H. Adams ms. Jamaica. Independently described by C. B. Adams (1845: 14) from Jamaica; his type specimens are MCZ 155909 (lectotype, Jacobson & Boss, 1973: 418, 458, pl. 61, fig. 17) and NHMUK 1845.3.5.327–330 (n = 4). *Brachypodella seminuda* (Philippi, 1845) (Pilsbry, 1903b: 92–94, pl. 5, figs. 41–42, 44). However, since the C. B. Adams paper is dated January 1845, while Philippi’s paper is dated October 1845, Philippi’s name is both a junior homonym and a junior synonym of the C. B. Adams name.

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“*fasciata*, *Cylindrella*” – Philippi, 1845t: 48 [9], pl. 2, fig. 7. Sherborn (1926: 2314) listed this as a Philippi name, but the name was made available as *Cyclostoma fasciata* Lamarck, 1822.

#### Achatinidae

*rhodostoma*, *Achatina* – Philippi, 1849j: 29–30 [7–8], pl. 2, fig. 2. Locality unknown. Syntype, NHMUK 1923.7.13.1. *Archachatina rhodostoma* (Philippi, 1849), from West Africa (Pilsbry, 1905a: 115–116, pl. 22, fig. 11); Bequaert (1950: 177–180), in the subgenus (*Calachatina*).

*suturalis*, *Achatina* – Philippi, 1849j: 29 [7], pl. 2, fig. 1. Locality unknown. Pilsbry (1905a: 111, pl. 25, fig. 25) erroneously thought that this was a junior homonym of “*A. suturalis* Pfeiffer, 1848”, and he renamed Philippi’s



species as *Archachatina marginata* Swainson var. *subsuturalis*. However, Bequaert (1950: 156) determined that Pfeiffer's 1848 usage was not a new species, but merely a new combination for what is now *Polyphemus suturalis* (Pfeiffer, 1838), a species no longer classified in the Achatinidae. *Achatina marginata* var. *suturalis* Philippi, 1849, from West Africa (Bequaert, 1950: 154–158).

#### Subulinidae

*columella*, *Bulimus* – Philippi, 1844u: 158 [8], pl. 2, fig. 7. Brazil. *Obeliscus sylvatica* var. *columella* (Philippi, 1844) (Pilsbry, 1906: 248–249, pl. 34, figs. 49–50), or as *Obeliscus columella* (Philippi, 1844) (Simone, 2006: 187, fig. 688).

*lucida*, *Achatina* – Philippi, 1858b: 22, *non* Poey, 1853 [Poey's species is now *Allopeas micra* (d'Orbigny, 1835)]. Isla Juan Fernandez, Chile.

#### Oleacinidae

*dilatatus*, *Polyphemus* – Philippi, 1836a: 141; published as "*Achatina algira* var.  $\beta$  *Polyphemus dilatatus* Ziegler." However, Ziegler's name was a manuscript name. Adopted as the valid name of a subspecies pursuant to ICZN Code Article 45.6.4.1 (1999) by Beck (1837: 78) (Zilch, 1980: 288, pl. 20, fig. 6). *Poiretia dilatata dilatata* (Philippi, 1836), from southern Italy and Sicily (Subai, 1980: 154–156, pl. 11, figs. 5–9; text-fig. 2).

#### Streptaxidae

*largillierti*, *Pupa* – Philippi, 1844z: 165–166. Bourbon Id.; Largilliert. Synonym of *Sinoennea* (*Indoennea*) *bicolor* (Hutton, 1834), from India and which has been introduced into tropical and subtropical regions around the world (Thompson, 2011: 201).

#### Systrophidae (Scolodontidae)

*andicola*, *Helix* – Philippi, 1866a: 39, *non* Pfeiffer, 1846. Talcalegue, Chile. Renamed as *Helix andium* Philippi, in Pfeiffer, 1867a (q.v.). *Happia andium* (Philippi, in Pfeiffer, 1867) (Gude, 1902: 233; 1903: 326, as "*andicola*").

*andium*, *Helix* – Philippi, in Pfeiffer, 1867a: 79, *nom. nov. pro Helix andicola* Philippi, 1866a, *non* Pfeiffer, 1846. *Happia andium* (Philippi,

in Pfeiffer, 1867) (Gude, 1902: 233; 1903: 326, as "*andicola*").

*cuzcana*, *Helix* – Philippi, 1869a: 37; Pfeiffer, 1869b: 476–477, pl. 102, figs. 22–24. Santa Cruz, Cuzco, Peru. *Happia cuzcana* (Philippi, 1869) (Gude, 1902: 234; 1903: 326; Ramírez et al., 2003: 276).

*decagyra*, *Helix* – Philippi, 1869a: 37–38; Pfeiffer, 1869b: 499, pl. 107, figs. 18–20. Between San Gregorio and Patipampa, east of Huancayo, Peru; Raimondi. *Systrophia* (*Systrophella*) *decagyra* (Philippi, 1869) (Ramírez et al., 2003: 277).

#### Plectopylidae

"*dextrorsa*, *Helix refuga* var." – Hanley & Theobald (1870: 7, pl. 13, fig. 9) erroneously attributed the variety "*dextrorsa*" to Philippi, but it was actually described by Benson (1860); Philippi, in discussing *H. refuga* (1847s: 2–3 [52–55], pl. 10, fig. 4), did not use that variety name. *Charsaecia dextrorsa* (Benson, 1860), from southeastern Burma (Páll-Gergely et al., 2015: 10).

#### Endodontidae

*ochsenii*, *Helix* – Philippi, 1855b: 215; 1856b: 91; 1856d: 153. San Juan, Valdivia, Chile; in trees. *Amphidoxa* (A.) *ochsenii* (Philippi, 1855) (Stuardo & Vega, 1985: 131; Letelier et al., 2003: 103).

*paupera*, *Helix* – Philippi, 1860a: 183 [1864b: 164], Zool. pl. 7, fig. 9. Atacama coast, Chile. Stuardo & Vega (1985: 132) transferred this to the Endodontidae, but as "*incertae sedis*" as its generic placement was uncertain. Miquel & Araya (2013: 230) noted that this species "may be conspecific with" their own *Stephacharopa calderaensis* n. sp. (Charopidae), but Philippi's species "remains unresolved" given the absence of type material and the inadequate description.

*zebrina*, *Helix* – Philippi, 1855b: 215; 1856b: 91; 1856d: 153–154. Valdivia, Chile; in trees & near Río Rahue. *Amphidoxa* (*Stephanoda*) *zebrina* (Philippi, 1855) (Stuardo & Vega, 1985: 132; Letelier et al., 2003: 103).

#### Milacidae

*nigricans*, *Parmacella* – Philippi, 1836a: x, 125, pl. 8, fig. 1, ex Schultz ms; 1844g: 102, as *Limax*. Palermo, Sicily, Italy. *Milax nigricans* (Philippi, 1836) (Falkner et al., 2001: 50).



## Zonitidae

*abscondita*, *Helix* – Philippi, 1855b: 217; 1856b: 93; 1856d: 157. Valdivia, Chile. Stuardo & Vega (1985: 133) transferred this to the Zonitidae, but as “incertae sedis” since its generic placement was uncertain.

*testae*, *Helix* – Philippi, 1844n: 104–105, “*nom. nov. pro Helix philippii* Aradas & Maggiore, 1843, ex Testa ms, *non Helix philippii* Gray, 1834”, but the two species names are not homonyms, so it was an unnecessary replacement name. Also covered in Philippi, 1845g: 28–29 [2–3], pl. 6, fig. 5. Type species (OD) of *Oxychilops* C. R. Boettger, 1930. Synonym of *Oxychilus canini* (Benoit, 1843).

## Helicarionidae

“*conus*, *Helix*” – Pfeiffer (1841: 39) credited this species to Philippi, but at this point it was a manuscript name (“ined.”) and should instead be credited to Pfeiffer, 1841, ex Philippi ms. Philippi (1842c: 11 [2], pl. 1, fig. 7) listed this as one of his own names one year later, and Sherborn (1925: 1501) did so as well. This taxon is the type species (SM Martens, 1867) of *Geotrochus* Hasselt, 1823, and (OD) of *Chiroktisma* Gude, 1913, a junior synonym (Pilsbry, 1935).

## Ariophantidae

*pfeifferi*, *Helix* (“*Nonina*”) – Philippi, 1845i: 62. China. *Xestina pfeifferi* (Philippi, 1845) (Yen, 1942: 270, pl. 26, fig. 190).

*resplendens*, *Helix* – Philippi, 1846z2: 192. Mergui Archipelago, Burma; Th. Philippi. Type species (OD) of *Sarika* Godwin-Austen, 1907. *Macrochlamys resplendens* (Philippi, 1846), also from China (Yen, 1942: 270).

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“*Nonina*” – Philippi, 1845i: 62. Misspelling of *Nanina* Gray, 1834 [*non Nanina* Risso, 1826].

## Limacidae

*umbrosus*, *Limax* – Philippi, 1844g: 102. New name for *Limax variegata* (Philippi, 1836a), *non* Draparnaud, 1801, and *non* Delle Chiaje, 1830, when he transferred it from *Parmacella*. Synonym of *Limax flavus* Linnaeus, 1758 (Tryon, 1885b: 200).

*valdivianus*, *Limax* – Philippi, 1858b: 22. Valdivia, Chile. Hoffmann (1935: 221) concluded that Philippi’s species was a junior synonym of either *Agriolimax laevis* (O. F. Müller, 1774) or of *A. agrestis* (Linnaeus, 1758), but anatomical study would be required to resolve this.

*variegata*, *Parmacella* – Philippi, 1836a: x, 125. Palermo, Val de Noto, Sicily, Italy. Renamed as *Limax umbrosus* Philippi, 1844g, when he transferred this species to *Limax*, where it became *non* Draparnaud, 1801, and *non* Delle Chiaje, 1830; Bivona (1839: 98) erroneously thought that Philippi’s name was also a synonym of Draparnaud’s 1801 name.

*virescens*, *Parmacella* – Philippi, 1836a: x, 125, pl. 8, fig. 2, ex Schultz ms; 1844g: 101, as *Limax*. Palermo, Sicily, Italy. *Limax virescens* (Philippi, 1836) (Tryon, 1885b: 213); unnecessarily renamed *Limax schultzii* Bivona (1839: 94–95).

## Vitrinidae

*birmanica*, *Vitrina* – Philippi, in Pfeiffer, 1847: 65. Mergui, Birma; Th. Philippi. *Helicarion birmanica* (Philippi, in Pfeiffer, 1847) (Tryon, 1885b: 177, pl. 41, fig. 42).

*valdiviana*, *Vitrina* – Philippi, 1858a: 123. Corral, Chile; Hermann Krause.

## Helicidae sensu latu

*bellula*, *Helix* – Philippi, 1858a: 124. Puerto Montt, Chile.

*erythrostroma*, *Helix* – Philippi, in Pfeiffer, 1850: 84. No locality provided.

*faunus*, *Helix* – Philippi, 1851b: 29–30. Mountains near Santa Fé de Bogota, Colombia. *Pleurodonte (Isomeria) faunus* (Philippi, 1851) (Pilsbry in Tryon & Pilsbry, 1889b: 137–138, pl. 46, figs. 21–23; 1894b: 94).

*fonki*, *Helix* – Philippi, 1858a: 124. Puerto Montt, Chile.

*globularis*, *Helix* – Philippi, 1836a: x, 127, ex Ziegler ms.; Rossmassler, 1838: 7, pl. 35, fig. 442; Philippi, 1844g: 104. Palermo, Sicily, Italy. *Marmorana globularis* (Philippi, 1836), from Sicily (Fiorentino et al., 2008: 810).

*grohmanni*, *Helix* – Philippi, 1836a: x, 128, pl. 8, fig. 5; 1844g: 104–105. Palermo, Sicily, Italy. *Helix (Iberus) grohmanni* Philippi, 1836 (Pilsbry, in Tryon & Pilsbry, 1889b: 205, pl. 54, fig. 7; Pilsbry, 1894b: 94).

*helvacea*, *Helix* – Philippi, 1845g: 27–28 [1–2], pl. 6, fig. 2. China; Largilliert. *Helix (Eulota)*



- ravida* Benson, 1842 (Tryon, in Tryon & Pilsbry, 1888b: 48, pl. 10, fig. 15; Pilsbry, 1895b: 205).
- laevula*, *Helix* – Philippi, 1858a: 123. Puerto Montt, Chile.
- merguiensis*, *Helix* – Philippi, 1846z2: 192. Mergui Archipelago, Burma; Th. Philippi. *Planispira* (*Trachea*) *gabata* (Gould 1843) (Tryon, in Tryon & Pilsbry, 1888b: 57, pl. 14, fig. 83; Pilsbry, 1894b: 116).
- montteana*, *Helix* – Philippi, 1858a: 123. Puerto Montt, Chile.
- osbeckii*, *Helix* – Philippi, in Pfeiffer, 1847: 65–66. China; Largilliert. *Helix* (*Plectotropis*) *osbecki* (Philippi, in Pfeiffer, 1847) (Tryon, in Tryon & Pilsbry, 1888b: 59).
- paciniana*, *Helix* – Philippi, 1836a: x, 127, pl. 8, fig. 9; 1844g: 105. Sicily, mountains. *Helix* (*Iberus*) *paciniana* (Philippi, 1836) (Pilsbry, in Tryon & Pilsbry, 1889b: 204, pl. 55, figs. 35–38), or as *Marmorana* (*Murella*) *scabriuscula paciniana* (Philippi, 1836) (Fiorentino et al., 2008).
- pencana*, *Helix* – Philippi, 1858b: 21. Concepción, Chile; Germain.
- pyramis*, *Helix* – Philippi, 1836a: xi, 135, pl. 8, fig. 20; 1844g: 111. Palermo, Sicily, Italy. Type species (SD Herrmannsen, 1847) of *Ochthe-philu* Beck, 1837. *Helix caroni* Deshayes var. *pyramis* Philippi, 1836 (Tryon, in Tryon & Pilsbry, 1888b: 30; Pilsbry, 1895b: 262).
- quisquilia*, *Helix* – Philippi, 1858a: 124. Valdivia, Chile.
- rhinion*, *Helix* – Philippi, 1858b: 21. Santiago or Concepción, Chile.
- segestana*, *Carocolla* – Philippi, 1836a (pre-April): 136, pl. 8, fig. 6; Rossmässler, 1836 (Sept. or later): 7, pl. 17, fig. 233 (as *Helix*); Philippi, 1844g: 105, as *Helix*. Mountains of western Sicily, Italy. *Marmorana* (*Murella*) *scabriuscula segestana* (Philippi, 1836) (Fiorentino et al., 2008).
- selinuntina*, *Carocolla* – Philippi, 1836a: xi, 136, pl. 8, fig. 11; 1844g: 105, as *Helix*. “Ad Thermas Selinuntinas” [hot springs], Sciacca, Sicily, Italy. *Iberus scabriuscula* Deshayes var. *selinuntina* (Philippi, 1836) (Pilsbry, in Tryon & Pilsbry, 1889b: 203, pl. 62, figs. 28–30), or as *Marmorana* (*Murella*) *scabriuscula selinuntina* (Philippi, 1836) (Fiorentino et al., 2008).
- sphaeroidea*, *Helix* – Philippi, 1836a: x, 135, pl. 8, fig. 19; 1844g: 112, 217. Palermo, Sicily, Italy; fossil.
- theodori*, *Helix* – Philippi, 1846z2: 191–192. Mergui Archipelago, Burma; Th. Philippi.

*Nanina theodori* (Philippi, 1846) (Tryon, 1886b: 83, pl. 16, fig. 25).

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- “*incei*, *Helix*” – Philippi, 1846f: 83 [35], pl. 7, fig. 1. Listed by Iredale (1937: 33) as a Philippi species, the description here as well as that in a contemporaneous journal account were signed by Pfeiffer.
- “*largillierti*, *Helix*” – Pfeiffer, 1849: 78–79, ex Philippi ms. Liew-Kiew, China [Ryukyu Islands, Japan]; Largilliert. This species, which has been credited to “Philippi, in Pfeiffer” by some workers, was indicated as “mss”, and is thus credited to Pfeiffer. It is the type species (OD) of *Luchuhadra* Kuroda & Habe, 1949.
- “*soluta*, *Helix*” – Philippi, 1836a: x, 129, pl. 8, fig. 15, ex Ziegler ms. Palermo, Sicily, Italy. So listed by Sherborn (1930: 6022), this is *Helix soluta* Rossmässler, 1832, a synonym of *Marmorana* (*Murella*) *platychela sicana* (A. Férussac, 1822).
- “*stelzneriana*, *Helix*” – Tryon (1887b: 43) and Pilsbry (1893d: 41) attributed this name to Philippi, but without citation of a description or source. Stuardo & Vega (1985: 130) listed this as a possible *nomen nudum*, which it is.
- “*strobiliana*, *Helix*” – Tryon (1887b: 43) and Pilsbry (1893d: 41) attributed this name to Philippi, but without citation of a description or source. Stuardo & Vega (1985: 130) listed this as a possible *nomen nudum*, which it is.

#### Bradybaenidae

- cecillei*, *Helix* – Philippi, in Pfeiffer, 1849z1: 82. Tien Tong, China. *Euhadra cecillei* (Philippi, in Pfeiffer, 1849) (Yen, 1939: 155, pl. 16, fig. 8; 1942: 286).
- chinensis*, *Helix* – Philippi, 1845g: 27 [1], pl. 6, fig. 1. Nanking, China; Largilliert. Type species (M) of *Aegista* Albers, 1850. *Aegista chinensis* (Philippi, 1845) (Yen, 1939: 144, pl. 15, fig. 1; 1942: 281).
- pyrrhizona*, *Helix* – Philippi, 1845g: 28 [2], pl. 6, fig. 4. Woosung, China; Largilliert. Type species (OD) of *Cathaica* Möllendorff, 1884.

#### Camaenidae (Pleurodontidae)

- crassula*, *Helix* – Philippi, 1844t: 152 [22], pl. 5, fig. 3. Java. *Chloritis crassula* (Philippi, 1844) (Schepman, 1912: 233–234).
- raimondii*, *Helix* – Philippi, 1867a: 65; Pfeiffer, 1867: 329–330, pls. 79, figs. 7–9. Between



Santa Batalina and Yanayaco, Loreto, Peru. *Labyrinthus raimondii* (Philippi, 1867) (Ramírez et al., 2003: 283).

#### Helminthoglyptidae

*alsophila*, *Helix* – Philippi, 1867a: 67; Pfeiffer, 1867: 329, pl. 79, figs. 4–6. Santa Ana, Peru; mountains. *Epiphragmophora alsophila* (Philippi, 1867) (Ramírez et al., 2003: 283).

*cuyana*, *Helix* – Philippi, in Pfeiffer, 1867a: 79, ex Strobel ms; Pfeiffer, 1867: 332–333, pl. 79, figs. 16–18; Pfeiffer, 1869a: 91. Mendoza, Peru. Synonym of *Epiphragmophora clausomphalos* (Deville & Hupé, 1850) (Ramírez et al., 2003: 282, authorship attributed to “Strobel in Pfeiffer”).

*huanucensis*, *Helix* – Philippi, 1867a: 65–66; Pfeiffer, 1867: 331–332, pl. 79, figs. 13–15. Huánuco, Peru. *Epiphragmophora huanucensis* (Philippi, 1867) (Ramírez et al., 2003: 284).

*pelliscolubri*, *Helix* – Philippi, 1867a: 66, as “*H. pellis columbri*”; Pfeiffer, 1867: 330–331, pl. 79, figs. 10–12. Otusco, Peru. Also indexed by Ruhoff (1980: 203) under *columbri*. *Epiphragmophora pelliscolubri* (Philippi, 1867) (Ramírez et al., 2003: 284).

*tschudiana*, *Helix* – Philippi, 1867a: 66; Pfeiffer, 1867: 328, pl. 79, figs. 1–3. Huancavelica, Peru. Synonym of *Epiphragmophora clausomphalos* (Deville & Hupé, 1850) (Ramírez et al., 2003: 282).

#### Hygromiidae

*elata*, *Carocolla* – Philippi, 1836a: 137, pl. 8, fig. 16, ex Férussac ms. Palermo, Sciacca, and Pachino, Sicily, Italy. Férussac’s material is in MNHN Paris (2 lots, one from Sicily; the other from “Caprée et Sicily”). Synonym of *Trochoidea caroni* (Deshayes, 1832) (Maio et al., 2013: 487, fig. 24). Férussac (1821) listed this species name, which he attributed to “Faure-Biguet”, but he did not provide a description, so it was a *nomen nudum*; Philippi was the first to make the name available.

*gargottae*, *Carocolla* – Philippi, 1836a: xi, 136–137, pl. 8, fig. 10; 1844g: 110, as *Helix*. Palermo & Termini, Sicily, Italy. Type species (SD Kobelt, 1892) of *Xerotropis Monterosato*, 1892. Synonym of *Cernuella rugosa* (Lamarck, 1822) (Manganelli et al., 1996: 1–17, figs. 3–6, 8–10, 12–26).

*limbata*, *Carocolla* – Philippi, 1836a: xi, 137, pl. 8, fig. 7. Palermo, Sicily, Italy.

*turrita*, *Carocolla* – Philippi, 1836a: xi, 137–138, pl. 8, fig. 17; 1844g: 111, as *Helix*. Palermo, Sicily, Italy. Syntypes, SMF 10307 (7.5 mm x 5.9 mm); SMF 304162 (n = 4). Synonym of *Trochoidea caroni* (Deshayes, 1832) (Maio et al., 2013: 487, fig. 24).

#### Pleurodontidae (Solaropsidae)

*incarum*, *Helix* – Philippi, 1869a: 36–37; Pfeiffer, 1869b: 475–476, pl. 102, figs. 19–21. Santa Cruz, Cuzco, Peru. *Psadara incarum* (Philippi, 1869) (Ramírez et al., 2003: 283).

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LITERATURE CITED

The first section of this Literature Cited includes all works by Philippi that cover molluscs, whether or not they contain new taxa, including contributions by Philippi to publications authored by others.

The references with a date or both a date and a letter code – the letter codes run up to z6 for one year! – and without an asterisk are works by Philippi, including books, sections of his *Abbildungen* or of the *Systematisches Conchylien-Cabinet*, as well as journal articles. Also included in this date-letter sequence is a work by Roemer (1849) containing a substantial block of descriptive text by Philippi. The date and letter codes allow the list of taxa to be correlated with particular entries in this bibliography. In some cases, the letter/date code includes more than one section of a work if there were no other Philippi items within that same period. Information on the month and dates is generally only known for the *Zeitschrift für Malakozoologie* (Kabat & Coan, 2016); for other publications where only the “month” is given, the publication date should be considered as the last day of that month.

Square brackets [ ] indicated the spanning dates of entire papers or sections. Dates in wavy brackets { } are the individual parts of these papers or sections cited under appropriate dates later in the list.

Works that have been mistakenly cited as sources of Philippi taxa are cited only in the Section II of the Literature Cited.

Citations with an asterisk (\*) in this section indicate works by other authors in which Philippi had a few, scattered descriptions, both first appearances of the taxa or subsequent treatments by Philippi himself. Full citations for some these works by other authors that include Philippi’s species descriptions, particularly in the *Systematisches Conchylien-Cabinet*, are included at the end of Section I in cases when the citation details are too lengthy and complex to be included in the main chronological sequence.

References for all other works cited in the list of taxa (i.e., the secondary literature) are included only in Section II of the Literature Cited. This includes near contemporaneous works containing discussions or figures of Philippi’s taxa.

I. Malacological Papers by Philippi and Other Sources Containing Philippi’s Molluscan Taxa

ANDREA, F., 1840, *Elogio storico del Barone Antonino Bivona Bernardi*. Palermo, Oretea, [ii] + 98 pp., frontispiece [pp. 88–89, letter from Philippi to Bivona, 12 April 1832].  
KÜSTER, H. C., 1844, 1847 [1844–1862], *Die Schliessschnecken und die verwandten Gattungen (Clausilia, Balea, Cylindrella, Megaspira.)*, mit Beiträgen von Dr. Philippi. In *Abbildungen nach der Natur mit Beschreibungen. Systematisches Conchylien-Cabinet*, 1(14): 1–355, pls. 1–38.

|       |      |      |         |          |            |
|-------|------|------|---------|----------|------------|
| Pp.   |      |      | 1–32    | 33–72    | 73–88      |
| Pls.  | 2    | 1    | 3, 4, 8 | 5, 9, 11 | 10, 12, 16 |
| Date  | 1844 | 1845 | 1847    | 1850     | 1852       |
| Lief. | 47   | 53   | 67      | 99       | 106        |

|       |                 |      |         |            |       |
|-------|-----------------|------|---------|------------|-------|
| Pp.   | 89–150          |      | 151–174 |            |       |
| Pls.  | 6, 7, 13–15, 19 |      | 18, 20  | 17, 21, 22 | 23–28 |
| Date  | 1853            | 1853 | 1854    | 1855       | 1857  |
| Lief. | 121             | 125  | 132     | 148        | 154   |

|       |         |         |         |         |         |
|-------|---------|---------|---------|---------|---------|
| Pp.   | 175–222 | 223–238 | 239–286 | 287–326 | 327–355 |
| Pls.  | 29–34   |         | 35–38   |         |         |
| Date  | 1860    | 1860    | 1861    | 1861    | 1862    |
| Lief. | 172     | 173     | 175     | 176     | 181     |

Collation sources: Woodward (1910: 1252); Smith & England (1937: 92); Johnson (1968: 364); Welter-Schultes (1999: 165). Date on title page is 1847.



KÜSTER, H. C., W. B. R. DUNKER & S. CLESSIN, 1841–1886, Die Familie der Limnaeiden enthaltend die Genera *Planorbis*, *Limnaeus*, *Physa* und *Amphipeplea*. In Abbildungen nach der Natur mit Beschreibungen. Mollusca Gasteropoda: Limnaeacea: Schlammschnecken. *Systematisches Conchylien-Cabinet*, 1(17)[(a)]: 1–34, 35a, 36a, 35–430, pls. 1–55.

|        |        |        |          |        |                |
|--------|--------|--------|----------|--------|----------------|
| Pp.    | 1–8    |        | 9–20     |        | 21–28, 35–62   |
| Pls.   |        | 1      | 2, 3, 16 | 4      | 5–10           |
| Date   | 1841   | 1843   | 1844     | 1844   | 1850           |
| Lief.  | 32     | 42     | 47       | 49     | 90             |
| Author | Küster | Küster | Küster   | Küster | Küster; Dunker |

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|        |                 |           |         |         |         |
|--------|-----------------|-----------|---------|---------|---------|
| Pp.    | 29–34, 35a, 36a | 63–94     | 95–110  | 111–150 | 151–182 |
| Pls.   |                 | 11–15, 17 | 18–22   | 23–27   | 28–33   |
| Date   | 1878            | 1882      | 1883    | 1884    | 1884    |
| Lief.  | 270             | 319       | 320     | 328     | 331     |
| Author | Clessin         | Clessin   | Clessin | Clessin | Clessin |

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|--------|---------|---------|---------|---------|---------|
| Pp.    | 183–222 | 223–278 | 279–310 | 311–358 | 359–430 |
| Pls.   | 34–39   | 40–44   | 45–50   | 51–55   |         |
| Date   | 1884    | 1885    | 1885    | 1886    | 1886    |
| Lief.  | 332     | 334     | 336     | 338     | 339     |
| Author | Clessin | Clessin | Clessin | Clessin | Clessin |

Collation sources: Woodward (1910: 1252); Smith & England (1937: 94); Johnson (1968: 364); Welter-Schultes (1999: 166–167). Date on title page is 1886. Pp. 1–28 authored by Küster; pp. 29–36a by Clessin; pp. 35–62 by Dunker, and pp. 63–end by Clessin, according to information in the MCZ copies. Smith & England (1937: 94) and Johnson (1968: 364) recorded that pages 35–36 were used twice in the page numbering.

PFEIFFER, L. C. G., 1841, 1846 [1841–1846], *Symbolae ad historiam heliceorum*. (Th. Fischer), Cassell, Part 1, 88 pp. (1841); Part 2, 147 pp. (1842); Part 3, 100 pp. (1846).

PFEIFFER, L. C. G., 1869a, Bemerkungen zu R. A. Philippi's Aufsatz: Diagnoses etc. *Malakozoologische Blätter*, 16(3): 88–91 (April) [for Pfeiffer, 1869b, see section II].

PHILIPPI, R. A., 1834a, Ueber das Thier der *Solenomya mediterranea*. *Archiv für Naturgeschichte*, 1(2): 271–276, pl. 4, figs. 1–5.

1834b, Über das Verhältniss der untergegangenen und lebenden Conchylien-Arten in Siciliens Tertiär-Bildungen. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, 1834: 516–519.

1836a, *Enumeratio molluscorum Siciliae cum viventium tum in tellure Tertiaria fossilium quae in itinere suo observavit*, vol. 1. Schroppi, Berolini [Berlin], xiv + 268 pp., 12 pls. (April 1836 or earlier) [vol. 2 = 1844g].

1836b, Beschreibung einiger neuen Conchylien-Arten and Bemerkungen über die Gattung *Lacuna* von Turton. *Archiv für Naturgeschichte*, 2(2): 224–235, pls. 7, 8.

1837a, *Pododesmus*, ein neues Genus der Acephalen. *Archiv für Naturgeschichte*, 3(1): 385–387, pl. 4, fig. 1.

1837b, *Pododesmus decipiens*, ein neues Genus der zweischaligen Mollusken. *Jahresbericht die Thätigkeit des Vereins für Naturkunde zu Cassel*, 1: 9–10.

1837c, Über die subfossilen Seethier-Reste von Pozzuoli bei Neapel und auf der Insel Ischia. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, 1837: 285–292, pl. 3, figs. 4, 5.

1837d, Beschreibung einer neuen Art *Nerinea* und einer neuen fossilen Art *Pecten*. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, 1837: 193–296, pl. 3, figs. 1–3, 6, 7.

1839a, Einige zoologische Notizen. 1, Zwei neue Arten von *Euplocamus*. *Archiv für Naturgeschichte*, 5(1): 113–115, 133 [pl. expl.], pl. 3, figs. 1, 2 [translated, *Annals and Magazine of Natural History* (n.s.) 4(22): 88–90, pl. 3, figs. 1, 2].

1839b, Einige zoologische Notizen. 2, Ueber das Thier von *Pileopsis garnoti* Payr[.]; *Patella garnoti* Phil. Emum. Moll. Siciliae. *Archiv für Naturgeschichte*, 5(1): 115–117, 133 [pl. expl.], pl. 3, fig. 3 [translated, *Annals and Magazine of Natural History* (n.s.) 4(22): 90–92, pl. 3, fig. 3; with rebuttal by J. E. Gray, 4(25): 305].

1839c, Einige zoologische Notizen. 3, Ueber das Thier von *Galeomma*. *Archiv für Naturgeschichte* 5(1): 117–119, 133 [pl. expl.], pl. 3, fig. 4 [translated, *Annals and Magazine of Natural History* (n.s.) 4(22): 92–93, pl. 3, fig. 4]. [Parts 4 and 5 of this series treated non-molluscan invertebrates.]



- 1839d, Einige zoologische Notizen. 6, *Pandorina corruscans* Scacchi. *Archiv für Naturgeschichte*, 5(1): 122–125, 133–134 [pl. expl.], pl. 4, figs. 1–5 [translated, *Annals and Magazine of Natural History* (n.s.) 4(25): 294–297, pl. 4, figs. 1–5; with rebuttal by J. E. Gray, 4(25): 305–306].
- 1839e, Einige zoologische Notizen. 7, Ueber das Thier von *Astarte incrassata* De la Jonk. *Archiv für Naturgeschichte*, 5(1): 125–127, 134 [pl. expl.], pl. 4, fig. 6 [translated, *Annals and Magazine of Natural History* (n.s.) 4(25): 298–299, pl. 4, fig. 6].
- 1839f, Einige zoologische Notizen. 8, Ueber das Thier von *Pleurotoma bertrandi* Payr. *Archiv für Naturgeschichte* 5(1): 127–127, 134 [pl. expl.], pl. 4, fig. 7 [translated, *Annals and Magazine of Natural History* (n.s.) 4(25): 299, pl. 4, fig. 7].
- 1839g, Einige zoologische Notizen. 9, Ueber Eier von *Vermetus gigas* Bivona. *Archiv für Naturgeschichte*, 5(1): 128, 134 [pl. expl.], pl. 4, fig. 8 [translated, *Annals and Magazine of Natural History* (n.s.) 4(25): 299–300, pl. 4, fig. 8]. [Last two parts of this series, 10 and 11, were on non-molluscan invertebrates.]
- 1839h, Notiz, die sogenannten Samenmaschinen des *Octopus* betreffend. *Archiv für Anatomie, Physiologie und Wissenschaftliche Medicin, in Verbindung mit mehreren Gelehrten*, 1839: 301–310, pl. 15.
- 1840a, Lettera del Sig. Rodolfo [sic] A. Philippi da Berlino Professore di Zoologia alla Scuola Politecnica di Cassel – al Dottor di Medicina Andrea Aradas. *Giornale del Gabinetto Letterario dell'Accademia Gioenia* (Catania), 5(5): 67–70 (July).
- 1840b, Zoologische Bemerkung. I. *Clavagella balanorum* Scacchi. *Archiv für Naturgeschichte*, 6(1): 181–184, pl. 3 [figs. 1–6] [pp. 184–195, rest of pl. 3 and all of pl. 4 on non-molluscan invertebrates] [translated, *Annals and Magazine of Natural History* (n.s.) 6(35): 89–101, pls. 3–4].
- \*1840, See also Andrea, F., above.
- 1841a, Zoologische Bemerkungen. *Archiv für Naturgeschichte*, 7(1): 42–59, pl. 5.
- 1841b, Bemerkungen über einige Linnéische Conchylien-Arten, welche von den spätern Conchyliologen verkannt sind. *Archiv für Naturgeschichte*, 7(1): 258–276.
- 1841c, Berichtigung von Berichtigungen. *Archiv für Naturgeschichte*, 7(1): 339–344.
- 1841d, *Trochus triumphans*. *Jahresbericht die Thätigkeit des Vereins für Naturkunde zu Cassel*, 5: 8.
- 1841e, *Trochus chinensis*. *Jahresbericht die Thätigkeit des Vereins für Naturkunde zu Cassel*, 5: 8–9.
- 1841f, *Ueber die Tertiärversteinerungen der Wilhelmshöhe bei Kassel*. Cassel, 32 pp. (August) [reprinted from the Programm der höheren Gewerb-Schule in Cassel für 1841–1842]. Reviewed in: *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, 1841: 613–614. Contents and pagination same as first 32 pp. of 1844z4, but with changes made in the latter on p. 24. Janssen & Kadolsky (2016) noted that Philippi (1844z4: 1) stated the publication date to be “August 1841,” so that “the likely publication date is early August 1841.”
- \*1841 {\*1843}, [Descriptions of three species of *Physa*]. Pp. 5–7 [1841], pl. 1 [1843], in: H. C. KÜSTER, W. B. R. DUNKER & C. CLESSIN, 1841–1886, *Die Familie der Limnaeiden* [See full citation above].
- \*1842, [See at end of this section under Philippi & Scacchi].
- 1842a {1843j, 1844v, 1847d, 1848e} [1842–1848], [Monograph on] *Melania*. *Abbildungen und Beschreibungen*, 1(1): 1–6, pl. 1 (August 1842) [n. sp.: Busch]; 1(3): 59–64, pl. 2 [n. spp.: Busch, Dunker & Philippi] (November 1843); 1(7): 159–164, pl. 3 [n. spp.: Busch & Dunker] (October 1844); 2(6): 169–177, pl. 4 [n. spp.: Busch, Meder, Megerle von Mühlfeld, Philippi] (February 1847); 3(3): 55–59, pl. 5 [n. spp.: Busch & Philippi] (February 1848) [also numbered: 1–27, 29–33].
- 1842b, [Monograph on] *Strombus*. *Abbildungen und Beschreibungen*, 1(1): 7, pls. 1, 2 [n. sp.: Philippi] (August 1842) [also numbered p. 1].
- 1842c {1843a, 1843g, 1844a, 1844t, 1845-l, 1846f, 1846v, 1847f, 1847s} [1842–1847], [Monograph on] *Helix* [including *Streptaxis*]. *Abbildungen und Beschreibungen*, 1(1): 9–12, pl. 1 [in text as “pl. 4”] (August 1842) [n. spp.: Busch & Philippi]; 1(2): 21–24, pl. 2 (February 1843) [n. spp.: Koch & Pfeiffer]; 1(3): 47–52, pl. 3 [n. spp.: Jonas & Dunker] (October 1843); 1(4): 77–81, pl. 4 [no n. sp.] (January 1844); 1(7): 151–155, pl. 5 [n. spp.: Koch, Pfeiffer & Philippi] (October 1844); 2(1): 1–8, pl. 6 [includes *Streptaxis*; n. spp.: Dunker, Pfeiffer & Philippi] (September 1845); 2(3): 83–87, pl. 7 [no n. sp.] (February 1846); 2(5): 127–131, pl. 8 [n. sp.: Pfeiffer] (October 1846); 2(7): 183–186, pl. 9 [no n. spp.] (March 1847); 3(1): 1–4, pl. 10 [no n. spp.] (August 1847) [also numbered pp. 1–19, 21–24, 27–39, 41–45, 47–54] [species in this part erroneously listed by Sherborn as being in part 6].
- 1842d {1845s} [1842–1845], [Monograph on] *Natica*. *Abbildungen und Beschreibungen*, 1(1): 13–17, pl. 1 (August 1842) [n. spp.: Busch & Philippi]; 2(2): 41–46, pl. 2 [n. sp.: Busch] (October 1845) [also numbered pp. 1–5, 7–12].
- 1842e {1847z3, 1848i, 1849f} [1842–1849], [Monograph on] *Unio*. *Abbildungen und Beschreibungen*, 1(1): 19–20, pl. 1 (August 1842) [n. sp.: Busch]; 1(3): 75, pl. 2 [n. sp.: Busch] (November 1843); 3(2): 45–47, pl. 3 [n. spp.: Parreyss & Philippi] (November 1847); 3(2): 49–50, pl. 4 (misnumbered as “VI”) [separate, consecutive section on *Unio*; n. sp.: Philippi] (November 1847); 3(3): 79–81, pl. 5 [n. spp.: Busch & Bronn] (February 1848); 3(4): 27–28, pl. 6 [no n. sp.] (January 1849) [also numbered pp. 1–2, [3], 5–7, 9–13, 15–16].
- 1842f {1845y, 1847z4, 1849z2, 1850p, 1852f} [1842–1852], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Turbo*, *Trochus*, *Solarium*, *Rotella*, *Delphinula*, *Phasianella*). In *Abbildungen nach der Natur mit Beschreibungen. Die Mondschncken: Turbo* Lin. *Systematisches Conchylien-Cabinet*, 2(2): I–II, 1–98, pls. A, 1–19.



|       |       |       |        |        |
|-------|-------|-------|--------|--------|
| Pp.   | 1–8   | 9–24  | 25–66  |        |
| Pls.  | 1–9   |       | 10–15  | 16, 18 |
| Date  | 1842f | 1845y | 1847z4 | 1849z2 |
| Lief. | 36    | 55    | 65     | 84     |

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|       |        |       |        |       |
|-------|--------|-------|--------|-------|
| Pp.   | 67–74  | 75–98 | I–II   |       |
| Pls.  | 17, 19 |       |        | A     |
| Date  | 1849z2 | 1850p | 1850p? | 1852f |
| Lief. | 86     | 93    | 93?    | 117   |

Collation sources: Woodward (1910: 1252); Oostingh (1925: 345); Smith & England (1937: 91); Johnson (1968: 365); Welter-Schultes (1999: 173). Date on title page is 1846. Despite the title page, this volume only covers *Turbo*. Pages I–II not mentioned in Woodward (1910: 1252) or Smith & England (1937: 91). Pages I–II contain species index (plate A not mentioned), could have been issued in Lief. 93, or shortly after.

1842g, Zoologische Beobachtungen. *Archiv für Naturgeschichte*, 8(1): 33–45, pl. 1 [only pp. 33–34 on molluscs; rest of paper, including plate, on non-molluscan invertebrates].

1843a, See [1842–1847], [Monograph on] *Helix* [including *Streptaxis*].

1843b, [Monograph on] *Neritina*. *Abbildungen und Beschreibungen*, 1(2): 25–30, pl. 1 (February 1843) [n. spp.: Busch, Pfeiffer & Philippi] [also numbered pp. 1–8].

1843c {1845p, 1847k, 1847x, 1849z, 1850i} [1843–1850], [Monograph on] *Arca*. *Abbildungen und Beschreibungen*, 1(2): 43–46, pl. 1 [n. sp.: Koch] (March 1843); 2(1): 29–32, pl. 2 [n. spp.: Jonas & Philippi] (September 1845); 2(7): 209–212, pl. 3 [n. sp.: Philippi] (March 1847); 3(1): 27–29, pl. 4 [n. sp.: Philippi] (September 1847); 3(6): 85–88, pl. 5 [n. sp.: Philippi] (October 1849); 3(7): 113–114, pl. 6 [no n. sp.] (April 1850) [also numbered pp. 1–22].

1843d {1843h, 1844c, 1844p, 1845a, 1845n, 1845r} [1843–1845], [Monograph on] *Trochus*. *Abbildungen und Beschreibungen*, 1(2): 31–34, pl. 1 [n. spp.: Koch, Anton & Philippi] (March 1843); 1(3): 65–69, pl. 2 [n. spp.: Jonas, Koch & Philippi] (November 1843); 1(4): 89–92, pl. 3 [n. spp.: Philippi & Menke] (January 1844); 1(6): 137–141, pl. 4 [plate mislabeled as “3”; n. spp.: Koch, Anton & Philippi] (“June 1844”, but a July 1844 issue date more likely); 1(8): 187–190, pl. 5 [pl. mislabeled as “4”; n. spp.: Dunker & Koch; new genus by Philippi] (January 1845); 2(1): 13–18, pl. 6 [pl. mislabeled as “5”; n. spp.: Anton, Koch & Philippi; some spp. mislabeled in text as pl. “7”] (September 1845); 2(2): 35–39, pl. 7 [n. spp.: Dunker & Philippi] (October 1845) [also numbered pp. 1–9, 15–19, 21–35].

1843e {1844m, 1844y, 1845v, 1846n, 1846z, 1848h, 1849e, 1849o, 1849y} [1843–1849], [Monograph on] *Venus*. *Abbildungen und Beschreibungen*, 1(2): 39–42, pl. 1 [n. spp.: Koch, Megerle von Mühlfeld & Philippi] (March 1843); 1(5): 127–129, pl. 2 [n. sp.: Philippi] (“April 1844”, but follows a section on *Tellina* dated June 1844, a more likely issue date); 1(7): 175–178, pl. 3 [n. sp.: Philippi] (November 1844); 2(2): 61–63, pl. 4 [no n. sp.] (November 1845); 2(4): 107–110, pl. 5 [n. sp.: Pfeiffer & Philippi] (August 1846); 2(5): 151–152, pl. 6 [n. sp.: Anton] (October 1846); 3(3): 75–78, pl. 7 [n. sp.: Philippi] (February 1848); 3(4): 21–25, pl. 8 [n. sp.: Koch] (January 1849); 3(5): 59–61, pl. 9 [no n. sp.] (“March 1849”, but follows a section dated April 1849, so an issue date of April 1849 more likely); 3(6): 81–84, pl. 10 [n. sp.: Philippi] (October 1849) [also numbered pp. 1–40].

1843f {1844u, 1845m, 1846o, 1846u, 1847a, 1847y, 1849a, 1850f} [1843–1850], [Monograph on] *Bulimus*. *Abbildungen und Beschreibungen*, 1(3): 53–58, pl. 1 [n. sp.: Jonas & Pfeiffer] (October 1843); 1(7): 157–158, pl. 2 [n. sp.: Dunker, Koch & Philippi] (October 1844); 2(1): 10–11, pl. 3 [n. sp.: Philippi] (September 1845); 2(4): 111–115, pl. 4 [n. sp.: Pfeiffer] (August 1846); 2(5): 123–126, pl. 5 [n. sp.: Pfeiffer] (October 1846); 2(6): 153–156, pl. 6 [n. sp.: Pfeiffer] (January 1847); 3(2): 31–33, pl. 7 [n. sp.: Pfeiffer] (November 1847); 3(4): 1–5, pl. 8 [no n. sp.] (January 1849); 3(7): 95–100, pl. 9 [no n. sp.] (April 1850) [also numbered pp. 1–8, 10–11, 13–17, 19–29, 35–39, 41–46] [species in this part erroneously listed by Sherborn as being in part 6].

1843g, See [1842–1847], [Monograph on] *Helix* [including *Streptaxis*].

1843h, See [1843–1845], [Monograph on] *Trochus*.

1843i {1844-l, 1846k, 1849n} [1843–1849], [Monograph on] *Tellina*. *Abbildungen und Beschreibungen*, 1(3): 71–73, pl. 1 [n. spp.: Jonas & Philippi] (November 1843); 1(5): 123–126, pl. 2 [n. spp.: Anton & Philippi] (June 1844); 2(1): 23–27, pl. 3 [no n. sp.] (September 1845); 2(4): 89–94, pl. 4 [n. sp.: Dunker & Krauss] (August 1846); 3(5): 55–57, pl. 5 [n. sp.: Philippi] (“March 1849”, but follows a section dated April 1849, so an issue date of April 1849 is more likely) [also numbered pp. 7–9, 11–19, 21–29; p. 14 misnumbered as “4”].

1843j, See [1842–1848], [Monograph on] *Melania*.

1843k {1847z2} [1843–1847], [Monograph on] *Solen*. *Abbildungen und Beschreibungen*, 1(2): 35–37, pl. 1 [n. spp.: Koch & Philippi] (1843); 3(2): 43–44, pl. 2 [n. sp.: Philippi] (November 1847) [also numbered pp. 1–6].



- 1843-l, Versteinerungen in Steinsalz. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, 1843: 568–569.
- \*1843 {1841}, [Descriptions of three species of *Physa*]. Pp. 5–7 [1841], pl. 1 [1843], in: H. C. KÜSTER, W. B. R. DUNKER & C. CLESSIN, 1841–1886, *Die Familie der Limnaeiden* [See full citation above].
- 1844a. See [1842–1847], [Monograph on] *Helix* [including *Streptaxis*].
- 1844b, [Monograph on] *Nerita*. *Abbildungen und Beschreibungen*, 1(4): 83–87; pl. 1 [n. spp.: Busch, Dunker & Philippi] (January 1844) [also numbered pp. 1–5].
- 1844c, See [1843–1845], [Monograph on] *Trochus*.
- 1844d, [Monograph on] *Pyrula*. *Abbildungen und Beschreibungen*, 1(4): 93–95; pl. 1 [n. spp.: Menke & Philippi] (January 1844) [also numbered pp. 1–3].
- 1844e {1845c} [1844–1845], [Monograph on] *Psammobia*. *Abbildungen und Beschreibungen* 1(4): 97–98, pl. 1 [n. sp.: Philippi] (January 1844); 1(8): 193–195, pl. 2 [n. spp.: Anton & Dunker] (January 1845) [also numbered pp. 1–5].
- 1844f {1845e} [1844–1845], [Monograph on] *Pecten*. *Abbildungen und Beschreibungen*, 1(4): 99–102, pl. 1 [n. spp.: Philippi] (January 1844); 1(8): 201–204, pl. 2 [no n. sp.] (“December 1844”, but follows section dated January 1845, a more likely issue date) [also numbered pp. 1–8].
- 1844g, *Enumeratio molluscorum Siciliae cum viventium tum in tellure Tertiaria fossilium quae in itinere suo observavit*, vol. 2. Anton, Halis Saxonum [Halle an der Saale, Germany], iv + 303 pp., pls. 13–28 (29 February, per Cretella ET AL., 2005: 15).
- 1844h, [Monograph on] *Steganotoma* et *Cyclostoma*. *Abbildungen und Beschreibungen*, 1(5): 103–106; pl. 1 [n. spp.: Busch & Philippi] (“March 1844”, but issued with a *Tellina* section dated June 1844, this is a more likely issue date) [also numbered pp. 1–4].
- 1844i {1845o, 1846p, 1847h, 1850j} [1844–1850], [Monograph on] *Fusus*. *Abbildungen und Beschreibungen*, 1(5): 107–112; pl. 1 [n. spp.: Anton, Busch, Dunker & Philippi] (“March 1844”, but with a section on *Tellina* dated June 1844, a more likely issue date); 2(1): 19–22, pl. 2 [n. sp.: Koch & Philippi] (September 1845); 2(4): 117–121, pl. 3 [n. spp.: Koch & Philippi] (August 1846); 2(7): 191–194, pl. 4 [n. spp.: Dunker & Philippi] (March 1847); 3(8): 115–120 [p. 120 misnumbered as 126], pl. 5 [n. sp.: Philippi] (September 1850) [also numbered pp. 1–15, 17–26].
- 1844j {1846w} [1844–1846], [Monograph on] *Paludina*. *Abbildungen und Beschreibungen*, 1(5): 113–118; pl. 1 [n. sp.: Busch] (June 1844); 2(5): 133–138, pl. 2 [n. sp.: Philippi] (October 1846) [also numbered pp. 1–12].
- 1844k {1844r, 1846b, 1847b, 1850d} [1844–1850], [Monograph on] *Haliotis*. *Abbildungen und Beschreibungen*, 1(5): 119–121; pl. 1 [n. sp.: Koch & Dunker] (June 1844); 1(6): 147–148, pls. 2, 3 [n. sp.: Philippi] (July 1844); 2(3): 69–70, pl. 4 [n. sp.: Philippi] (February 1846); 2(6): 157–158, pls. 5, 6 [no n. sp.] (January 1847); 2(8): 219–220, pls. 7, 8 [no n. sp.] (April 1847); 3(7): 89–92, pl. 9 [n. sp.: Philippi] (April 1850) [also numbered pp. 1–2, 4–16].
- 1844-l, See [1843–1849], [Monograph on] *Tellina*.
- 1844m, See [1843–1849], [Monograph on] *Venus*.
- 1844n, Nachtrag zum zweiten Bande der *Enumeratio Molluscorum Siciliae*. *Zeitschrift für Malakozoologie*, 1(7): 100–112 (30 July).
- 1844o, [Monograph on] *Glandina*. *Abbildungen und Beschreibungen*, 1(6): 131–134, pl. 1 [n. sp.: Pfeiffer & Jonas] (July 1844) [also numbered pp. 1–5].
- 1844p, See [1843–1845], [Monograph on] *Trochus*.
- 1844q, [Monograph on] *Sigaretus*. *Abbildungen und Beschreibungen*, 1(6): 143–146, pl. 1 [n. sp.: Philippi] (July 1844) [also numbered pp. 1–4].
- 1844r, See [1844–1850], [Monograph on] *Haliotis*.
- 1844s {1844x, 1845d, 1846-l, 1847e, 1847p, 1847w, 1848g} [1844–1848], [Monograph on] *Cytherea*. *Abbildungen und Beschreibungen*, 1(6): 149–150, pl. 1 [n. sp.: Koch] (July 1844); 1(7): 169–173, pl. 2 [n. sp.: Philippi] (October 1844); 1(8): 197–200, pl. 3 [n. spp.: Koch & Philippi] (January 1845); 2(4): 95–97, pl. 4 [no n. sp.] [misabeled as pl. 3 in text and on pl.] (August 1846); 2(6): 179–182, pl. 5 [misabeled as pl. 4 on pl.] [no n. sp.] (February 1847); 2(8): 299–231, pl. 6 [pl. misabeled as 5], pl. 7 [pl. misabeled as 6] [n. spp.: Philippi] (April 1847); 3(1): 23–25, pl. 8 [n. sp.: Philippi] (September 1847); 3(3): 71–74, pl. 9 [n. sp.: Philippi] (February 1848) [also numbered pp. 1–42].
- 1844t, See [1842–1847], [Monograph on] *Helix* [including *Streptaxis*].
- 1844u, See [1843–1850], [Monograph on] *Bulimus*.
- 1844v, See [1842–1848], [Monograph on] *Melania*.
- 1844w {1846c, 1850o} [1844–1850], [Monograph on] *Mactra*. *Abbildungen und Beschreibungen*, 1(7): 165–167, pl. 1 [n. sp.: Philippi] (October 1844); 2(3): 71–74, pl. 2 [n. sp.: Philippi] (February 1846); 3(8): 135–138, pl. 3 [n. sp.: Philippi] (November 1850) [also numbered pp. 1–12].
- 1844x, See [1844–1848], [Monograph on] *Cytherea*.
- 1844y, See [1843–1849], [Monograph on] *Venus*.
- 1844z, Descriptiones testaceorum quorundam novorum, maxime chinensium. *Zeitschrift für Malakozoologie*, 1(11): 161–167 (30 November).
- 1844z1 {1845t, 1847n, 1847t} [1844–1847], [Monograph on] *Cylindrella*. *Abbildungen und Beschreibungen*, 1(8): 179–186; pl. 1 [n. sp.: Pfeiffer & Dunker] (December 1844); 2(2): 47–53, pl. 2 [n. sp.: Pfeiffer] (October 1845); 2(8): 217–218 [under *Achatina*; p. 218 misnumbered as 219; n. sp. by



- Pfeiffer] (April 1847); 3(1): 5–8, pl. 3 [n. sp.: Pfeiffer] (August 1847) [also numbered pp. 1–18, not including added pp. under *Achatina*].
- 1844z2, Bemerkung über die Molluskenfauna Unter-Italiens. *Archiv für Naturgeschichte*, 10(1): 28–52, 348–370 [p. 32 misnumbered as “23”] [translated as: “Remarks on the molluscos animals of south Italy, in reference to the geographical extension of the Mollusca, and to the Mollusca of the Tertiary Period” in: *The Quarterly Journal of the Geological Society of London*, 1(2): 95–111, 1845; and as: “Remarks on the molluscos animals of south Italy, in reference to the Mollusca of the Tertiary Period” in: *The Quarterly Journal of the Geological Society of London*, 2(2): 1–17, 1846; second section only translated as “Comparative remarks on the Recent and fossil Mollusca of the south of Italy, and more particularly of Sicily” in: *The Edinburgh New Philosophical Journal*, 38(76): 202–214, April 1845].
- 1844z3, *Osservazioni intorno alla fauna de’ molluschi del regno delle due Sicilia ricavate da una lettera del Professori Philippi di Cassel al Professore Scacchi*. This seems to be a “stand alone” typeset version of a handwritten letter of November 2, 1844. Aradas (1870: 14–15) makes reference to it without indicating a journal, whereas for the similar, earlier letter from Philippi to him (1840a), he indicated a journal. The present letter, which does not mention any new taxa, does not appear in that journal in late 1844 or in 1845.
- 1844z4 [“1843”], *Beiträge zur Kenntniss der Tertiäerversteinerungen des nordwestlichen Deutschlands*. Theodor Fischer, Kassel, i–iii–[iv] + 1–85–[87] pp., 4 pls. Although this work is dated 1843 on the title page, with a preface dated 5 March 1843, it was not published until late 1844 due to Philippi’s delays in preparing the plates (Bronn, 1845: 510; Janssen & Kadolsky, 2016). Contents and pagination of the first 32 pages the same as 1841f, but with changes on p. 24.
- \*1844, See Küster, 1844–1862, *Systematisches Conchylien-Cabinet – Clausilia* [See full citation at the beginning of this section].
- 1845a, See [1843–1845], [Monograph on] *Trochus*.
- 1845b {1847z1} [1845–1847], [Monograph on] *Murex*. *Abbildungen und Beschreibungen*, 1(8): 191–192; pl. 1 [n. sp.: Philippi] (January 1845); 3(2): 39–42, pl. 2 [n. sp.: Philippi] (November 1847) [also numbered pp. 1–6].
- 1845c, See [1844–1845], [Monograph on] *Psammobia*.
- 1845d, See [1844–1848], [Monograph on] *Cytherea*.
- 1845e, See [1844–1845], [Monograph on] *Pecten*.
- 1845f, [viii] pp. – Register to Vol. 1 of *Abbildungen und Beschreibungen* – January 1845 [date of last sections].
- \*1845, [List and descriptions of Tertiary fossils]. Pp. 33–37, in: G. H. O. VOLGER, 1845 (April) [See full citation at end of this section].
- 1845g, Bemerkungen über die Mollusken-Fauna von Massachusetts. *Zeitschrift für Malakozoologie*, 2(5): 68–79 (30 June).
- 1845h, Kritische Bemerkung über einige *Trochus*-Arten und die Gattung *Axius*. *Zeitschrift für Malakozoologie*, 2(6): 87–91 (30 June).
- 1845i, Diagnosen einiger neuen Conchylien. *Archiv für Naturgeschichte*, 11(1): 50–71 [cited in an October monograph in the *Abbildungen*] (September).
- 1845j, Berichtigung zu Diagnosen neuer Conchylien. *Archiv für Naturgeschichte*, 11(1): 142–144 (September).
- 1845k, Bemerkung über einige Muschelgeschlechter, deren Thiere wenig bekannt sind. *Archiv für Naturgeschichte*, 11(1): 185–196, pl. 7 (September).
- 1845-l, See [1842–1847], [Monograph on] *Helix* [including *Streptaxis*].
- 1845m, See [1843–1850], [Monograph on] *Bulimus*.
- 1845n, See [1843–1845], [Monograph on] *Trochus*.
- 1845o, See [1844–1850], [Monograph on] *Fusus*.
- 1845p, See [1843–1850], [Monograph on] *Arca*.
- 1845q {1846a} [1845–1846], [Monograph on] *Fissurella*. *Abbildungen und Beschreibungen*, 2(2): 33–34, pl. 1 [n. sp.: Philippi] (October 1845); 2(3): 65–67, pl. 2 [n. spp.: Dunker & Philippi] (February 1846) [also numbered pp. 1–2].
- 1845r, See [1843–1845], [Monograph on] *Trochus*.
- 1845s, See [1842–1845], [Monograph on] *Natica*.
- 1845t, See [1844–1847], [Monograph on] *Cylindrella*.
- 1845u, [Monograph on] *Astarte*. *Abbildungen und Beschreibungen*, 2(2): 55–60, pl. 1 [n. sp.: Jonas] (October) [also numbered pp. 1–6].
- 1845v, See [1843–1849], [Monograph on] *Venus*.
- 1845w, Diagnoses [*sic*] testaceorum quorundam novorum. *Zeitschrift für Malakozoologie*, 2(10): 147–152 (30 November).
- 1845x, Ueber *Lucina edentula*. *Zeitschrift für Malakozoologie*, 2(12): 179–181 (31 December).
- 1845y, See [1842–1852], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Turbo*).
- 1845z, Verzeichniss der in der Gegend von Magdeburg bei Osterweddingen und Westeregeln vorkommenden Tertiär-Versteinerungen. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, 1845: 447–451.



1846a, See [1845–1846], [Monograph on] *Fissurella*.  
1846b, See [1844–1850], [Monograph on] *Haliotis*.  
1846c, See [1844–1850], [Monograph on] *Mactra*.  
1846d {1849x, 1850h} [1846–1850], [Monograph on] *Cyrena*. *Abbildungen und Beschreibungen*, 2(3): 75–79, pl. 1 [n. spp.: Philippi & Parreyss] (February 1846); 3(6): 77–79, pl. 2 [n. spp.: Busch & Philippi] (October 1849); 3(7): 107–111, pl. 3 [n. spp.: Busch & Philippi] (April 1850) [also numbered pp. 1–15].  
1846e, [Monograph on] *Ostrea*. *Abbildungen und Beschreibungen*, 2(3): 81–82, pl. 1 [no n. sp.] (February 1846) [also numbered pp. 1–2].  
1846f, See [1842–1847], [Monograph on] *Helix* [including *Streptaxis*].  
1846g, Descriptions of a new species of *Trochus*, and of eighteen new species of *Littorina*, in the collection of H. Cuming, Esq. *Proceedings of the Zoological Society of London*, for 1845 [13](154): 138–143 (February).  
1846h, Diagnosen einiger neuen Conchylien-Arten. *Zeitschrift für Malakozoologie*, 3(2): 19–24 (28 February); 3(4): 49–55 (30 April).  
1846i, Diagnoses testaceorum quorundam novorum. *Zeitschrift für Malakozoologie*, 3(7): 97–106 (31 July).  
1846j, Kritische Bemerkungen über die von Eschscholtz aufgestellten Arten von *Acmaea*. *Zeitschrift für Malakozoologie*, 3(7): 106–108 (31 July).  
1846k, See [1843–1849], [Monograph on] *Tellina*.  
1846-l, See [1844–1848], [Monograph on] *Cytherea*.  
1846m {1846x, 1847b1, 1847i, 1847o, 1847u, 1848f} [1846–1848], [Monograph on] *Litorina* [sic; Menke, 1828, incorrect subsequent spelling of *Littorina*]. *Abbildungen und Beschreibungen*, 2(4): 99–104, pl. 1 [no n. sp.] (August 1846); 2(5): 139–145, pl. 2 [n. spp. & var.: Menke & Philippi] (October 1846); 2(6): 159–167, pl. 3 [n. sp.: Krauss & Philippi] (January 1847); 2(7): 195–203, pl. 4 [n. sp.: Krauss & Philippi] (March 1847); 2(8): 221–225, pl. 5 [n. sp. & var.: Philippi] (April 1847); 3(1): 9–18, pl. 6 [n. sp.: Jonas & Philippi] (September 1847); 3(3): 61–69, pl. 7 [n. sp.: Philippi] (February 1848) [also numbered pp. 1–7, 9–25, 27–35, 37–43, 45–63].  
1846n, See [1843–1849], [Monograph on] *Venus*.  
1846o, See [1843–1850], [Monograph on] *Bulimus*.  
1846p, See [1844–1850], [Monograph on] *Fusus*.  
1846q, Ueber *Tornatella abbreviata*, *Otodus mitis*, *Otodus catticus* und *Myliobatis testae*. *Palaeontographica*, 1(1): 23–25, 337 [pl. expl.], pl. 2 (August) [only p. 23, pl. 2, fig. 1a, b, concerns *Tornatella*; other species are sharks].  
1846r {1847-l} [1846–1847], Verzeichniss der in der Gegend von Magdeburg aufgefundenen Tertiärversteinerungen. *Palaeontographica*, 1(1): 42–44 (August 1846); (2): 45–90, 337–338 [plate explanations], pls. 7–10, 10a (March 1847). A preliminary version published in the *Programm der höheren Gewerbschule in Cassel, 1846–1847*, 17 pp. (published between 9 July 1846 and 10 August 1846, fide Janssen & Kadolsky, 2016).  
1846s, *Bembicium novum* genus molluscorum gastropodorum. *Zeitschrift für Malakozoologie*, 3(9): 129–133 (30 September).  
1846t, Ueber *Turbo argyrostomus* L. *Zeitschrift für Malakozoologie*, 3(9): 133–135 (30 September).  
1846u, See [1843–1850], [Monograph on] *Bulimus*.  
1846v, See [1842–1847], [Monograph on] *Helix* [including *Streptaxis*].  
1846w, See [1844–1846], [Monograph on] *Paludina*.  
1846x, See [1846–1848], [Monograph on] *Litorina*.  
1846y {1847v} [1846–1847], [Monograph on] *Modiola*. *Abbildungen und Beschreibungen*, 2(5): 147–150, pl. 1 [n. sp.: Philippi] (October 1846); 3(1): 19–22, pl. 2 [no n. sp.] (September 1847) [also numbered pp. 1–8].  
1846z, See [1843–1849], [Monograph on] *Venus*.  
1846z1, Bericht über einige Französische Lokalfaunen der Land- und Süßwasser-Mollusken [reviews of papers by Joba, Dupuy, and Mermet]. *Zeitschrift für Malakozoologie*, 3(10): 154–157 (31 October).  
1846z2, Vier neue Konchylienarten. *Zeitschrift für Malakozoologie*, 3(12): 191–192 (31 December).  
1846z3 {1847z5, 1848-k, 1849z3, 1850q, 1851e, 1852d, 1855c} [1846–1855], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Turbo*, *Trochus*, *Solarium*, *Rotella*, *Delphinula*, *Phasianella*). In *Abbildungen nach der Natur mit Beschreibungen*. *Systematisches Conchylien-Cabinet*, 2(3): 1–372, pls. 1–49.

|       |        |        |        |        |        |        |
|-------|--------|--------|--------|--------|--------|--------|
| Pp.   | 1–24   |        | 25–32  |        | 33–40  |        |
| Pls.  | 1–6    | 7–12   |        | 13–18  |        | 19–24  |
| Date  | 1846z3 | 1847z5 | 1847z5 | 1847z5 | 1848-k | 1848-k |
| Lief. | 62     | 69     | 71     | 72     | 75     | 76     |



|       |        |        |                |         |       |         |
|-------|--------|--------|----------------|---------|-------|---------|
| Pp.   | 41–72  |        | 73–104         | 105–120 |       | 121–136 |
| Pls.  |        | 25–30  | 31, 32, 34, 35 | 36–39   | 40–45 |         |
| Date  | 1848-k | 1849z3 | 1849z3         | 1849z3  | 1850q | 1850q   |
| Lief. | 79     | 80     | 84             | 86      | 93    | 98      |

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|-------|---------|-----------|---------|---------|---------|--|
| Pp.   | 137–184 | 185–232   | 233–248 | 249–312 | 313–372 |  |
| Pls.  |         | 33, 46–49 |         |         |         |  |
| Date  | 1851e   | 1851e     | 1852d   | 1855c   | 1855c   |  |
| Lief. | 101     | 103       | 108     | 142     | 144     |  |

Collation sources: Woodward (1910: 1252); Smith & England (1937: 91); Johnson (1968: 365); Welter-Schultes (1999: 173–174). Date on title page is 1846. Despite the title page, this volume only covers *Trochus*.

- \*1846, See Pfeiffer (1841–1846), *Symbolae* [at the beginning of this section].
- 1847a, See [1843–1850], [Monograph on] *Bulimus*.
- 1847b, See [1844–1850], [Monograph on] *Haliotis*.
- 1847b1, See [1846–1848], [Monograph on] *Litorina*.
- 1847c, Versuch einer systematischen Eintheilung des Geschlechtes *Trochus*. *Zeitschrift für Malakozoologie*, 4(1): 3–11 (31 January); (2): 17–24 (28 February).
- 1847d, See [1842–1848], [Monograph on] *Melania*.
- 1847e, See [1844–1848], [Monograph on] *Cytherea*.
- 1847f, See [1842–1847], [Monograph on] *Helix* [including *Streptaxis*].
- 1847g, [Monograph on] *Purpura*. *Abbildungen und Beschreibungen*, 2(7): 187–190, pl. 1 [no n. sp] (March) [also numbered pp. 1–4].
- 1847h, See [1844–1850], [Monograph on] *Fusus*.
- 1847i, See [1846–1848], [Monograph on] *Litorina*.
- 1847j {1850g} [1847–1850], [Monograph on] *Lucina*. *Abbildungen und Beschreibungen*, 2(7): 205–207, pl. 1 [n. sp.: Jonas & Philippi] (March 1847); 3(7): 101–105, pl. 2 [n. sp.: Philippi] (April 1850) [also numbered pp. 1–9].
- 1847k, See [1843–1850], [Monograph on] *Arca*.
- 1847-l, See [1846–1847], Verzeichniss der in der Gegend von Magdeburg ...
- 1847m {1849j} [1847–1849], [Monograph on] *Achatina*. *Abbildungen und Beschreibungen*, 2(8): 213–218, pl. 1 [pp. 217–218 on *Cylindrella*, with p. 218 misnumbered as 219] [n. sp. of *Cylindrella*: Pfeiffer] (April 1847); 3(5): 29–31, pl. 2 [n. sp.: Philippi] (April 1849) [also numbered pp. 1–9].
- 1847n, See [1844–1847], [Monograph on] *Cylindrella*.
- 1847o, See [1846–1848], [Monograph on] *Litorina*.
- 1847p, See [1844–1848], [Monograph on] *Cytherea*.
- 1847q, [viii] pp. – Register to *Abbildungen und Beschreibungen* Vol. 2 – April 1847 [date of last dated sections in vol.].
- \*1847, [Descriptions of new species]. Pp. 65, 66, 68 and 84, in: L. C. G. PFEIFFER, ed., Diagnosen neuer Heliceen [collected descriptions of several new species by various authors; two of four parts]. *Zeitschrift für Malakozoologie*, 4(5): 65–71 (31 May); (6): 81–84 (30 June).
- 1847r {1848b, 1848c} [1847–1848], Testaceorum novorum centuria. *Zeitschrift für Malakozoologie*, 4(5): 71–77 (31 May 1847); 4(5): 84–96 (30 June 1847); 4(7): 113–127 (31 July 1847); 5(1): 13–16 (31 January 1848); 5(2): 17–27 (29 February 1848).
- 1847s, See [1842–1847], [Monograph on] *Helix* [including *Streptaxis*].
- 1847t, See [1844–1847], [Monograph on] *Cylindrella*.
- 1847u, See [1846–1848], [Monograph on] *Litorina*.
- 1847v, See [1846–1847], [Monograph on] *Modiola*.
- 1847w, See [1844–1848], [Monograph on] *Cytherea*.
- 1847x, See [1843–1850], [Monograph on] *Arca*.
- 1847y, See [1843–1850], [Monograph on] *Bulimus*.
- \*1847, [Description of one new species]. Pp. 149–150, in: L. C. G. PFEIFFER, ed., Diagnosen neuer Landschnecken [collected descriptions of several new species by various authors]. *Zeitschrift für Malakozoologie*, 4(10): 145–151 (31 October).
- 1847z {1849c} [1847–1849], [Monograph on] *Dolium*. *Abbildungen und Beschreibungen*, 3(2): 35–37, pl. 1 [n. sp.: Philippi] (November 1847); 3(4): 11–12, pl. 2 [n. sp.: Philippi] (January 1849) [also numbered pp. 1–6].
- 1847z1, See [1845–1847], [Monograph on] *Murex*.
- 1847z2, See [1843–1847], [Monograph on] *Solen*.
- 1847z3, See [1842–1849], [Monograph on] *Unio*.



- 1847z4, See [1842–1852], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Turbo*).
- 1847z5, See [1846–1855], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Trochus*).
- 1847z6, Beschreibung zweier neuer Conchyliengeschlechter, *Dibaphus* und *Amphichaena*, nebst einigen Bemerkung über *Cyamium*, *Ervilia* und *Entodesma*. *Archiv für Naturgeschichte*, 13(1): 61–66, pl. 3 (November) [partial translation in *Annals and Magazine of Natural History*, (Ser. 1), 19(128): 425–426].
- \*1847, See Küster, 1844–1862, *Systematisches Conchylien-Cabinet – Clausilia* [near the beginning of this section, p. 218].
- 1848a, Beschreibung zweier neuer Conchylien aus der Sammlung des Herrn Consul Gruner in Bremen. *Zeitschrift für Malakozoologie*, 5(1): 12–13 (31 January).
- 1848b, 1848c, See [1847r–1848], Testaceorum novorum centuria. *Zeitschrift für Malakozoologie*, 5(1): 13–16 (31 January 1848); 5(2): 17–27 (29 February 1848).
- 1848d, [Monograph on] *Oliva*. *Abbildungen und Beschreibungen*, 3(3): 51–54, pl. 1 [n. sp.: Philippi] (February 1848) [also numbered pp. 1–4].
- 1848e, See [1842–1848], [Monograph on] *Melania*.
- 1848f, See [1846–1848], [Monograph on] *Litorina*.
- 1848g, See [1844–1848], [Monograph on] *Cytherea*.
- 1848h, See [1843–1849], [Monograph on] *Venus*.
- 1848i, See [1842–1849], [Monograph on] *Unio*.
- 1848j, Ueber die neuen Gattungen und Arten der Conchylien welche in Griffith's englischer Ausgabe von Cuvier's Thierreich vorkommen. *Zeitung für Zoologie, Zootomie und Physiologie*, 1(11): 85–87 (11 March).
- 1848k, See [1846–1855], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Trochus*).
- 1849a, See [1843–1850], [Monograph on] *Bulimus*.
- 1849b {1849k, 1849v}, [Monograph on] *Patella* ["sive *Acmaea*" in first section]. *Abbildungen und Beschreibungen*, 3(4): 7–9, pl. 1 [n. sp.: Philippi] (January); (5): 33–39, pl. 2 [n. sp.: Philippi] (April?); 3(6): 71–72, pl. 3 [n. sp.: Philippi] (October) [also numbered 1–3, 5–11, 13–14].
- 1849c, See [1847–1849], [Monograph on] *Dolium*.
- 1849d, [Monograph on] *Cerithium*. *Abbildungen und Beschreibungen*, 3(4): 13–20, pl. 1 [n. sp.: Philippi] (January 1849) [also numbered pp. 1–8].
- 1849e, See [1843–1849], [Monograph on] *Venus*.
- 1849f, See [1842–1849], [Monograph on] *Unio*.
- 1849g, Kurze Beschreibung einiger neuen Conchylien. *Zeitschrift für Malakozoologie*, 5(7): 97–98 (31 January).
- 1849h, Centuria altera testaceorum novorum. *Zeitschrift für Malakozoologie*, 5(7): 99–112 (31 January 1849); 5(8): 123–128 (31 March 1849); 5(9): 129–144 (31 March 1849); 5(10): 145–150 (31 March 1849) [issues 7, 9 and 10 mislabeled as "1848" on title pages, with footer pages at ends of some issues giving correct year; includes species by Anton, Koch, Menke & Busch].
- 1849i {1849p, 1849r}, Centuria tertia testaceorum novorum. *Zeitschrift für Malakozoologie*, 5(10): 151–160 (31 March 1849); 5(11): 161–176 (31 March 1849); 5(12): 186–192 (April 1849); 6(2): 17–26 (May 1849).
- 1849j, See [1847–1849], [Monograph on] *Achatina*.
- 1849k, See 1849b ..., [Monograph on] *Patella*.
- 1849-l {1849u}, [Monograph on] *Buccinum*. *Abbildungen und Beschreibungen*, 3(5): 41–50, pl. 1 [n. sp.: Koch & Philippi] (April 1849); 3(6): 63–70, pl. 2 [n. sp.: Dunker & Philippi] (October 1849) [also numbered pp. 1–18].
- 1849m {1850m} [1849–1850], [Monograph on] *Pholas*. *Abbildungen und Beschreibungen*, 3(5): 51–53, pl. 1 [n. sp.: Philippi] (April 1849); 3(8): 127–130, pl. 2 [no n. sp.] (November 1850) [also numbered pp. 1–8].
- 1849n, See [1843–1849], [Monograph on] *Tellina*.
- 1849o, See [1843–1849], [Monograph on] *Venus*.
- 1849p, See 1849i, ... Centuria tertia testaceorum novorum. *Zeitschrift für Malakozoologie*, 5(12): 186–192 (30 April).
- 1849q, [Review of] Die südafrikanischen Mollusken [by Ferdinand Krauss]. *Zeitschrift für Malakozoologie*, 6(1): 1–3 (31 May).
- 1849r, See 1849i, ... Centuria tertia testaceorum novorum. *Zeitschrift für Malakozoologie*, 6(2): 17–26 (31 May).
- 1849s, 1849t {1851b} [1849–1851], Centuria quarta testaceorum novorum. *Zeitschrift für Malakozoologie*, 6(2): 27–32 (31 May 1849); 6(3): 33–35 (31 July 1849); 8(2): 29–32 (30 June 1851); 8(3): 39–48 (15 July 1851); 8(4): 49–64 (15 July 1851); 8(5): 65–74 (31 July 1851) [includes species by Menke & Jonas].
- 1849t, See 1849s, ... Centuria quarta testaceorum novorum. *Zeitschrift für Malakozoologie*, 6(3): 33–35 (31 July 1849) [erroneously titled as "Centuria tertia" and species incorrectly numbered as 118–122 instead of 18–22].



1849u, See 1849-l, ... [Monograph on] *Buccinum*.  
1849v, See 1849 b, ... [Monograph on] *Patella*.  
1849w {1850e, 1850k} [1849–1850], [Monograph on] *Fasciolaria*. *Abbildungen und Beschreibungen*, 3(6): 73–75, pl. 1 [n. sp.: Jonas] (October 1849); 3(7): 93–94, pl. 2 (April 1850) [n. sp.: Jonas]; 3(8): 121–122, pl. 3 (September 1850) [n. sp.: Jonas] [also numbered pp. 1–3, 5–8].  
1849x, See [1846–1850], [Monograph on] *Cyrena*.  
1849y, See [1843–1849], [Monograph on] *Venus*.  
1849z, See [1843–1850], [Monograph on] *Arca*.  
\*1849z1, [Description of *Helix cecillei*], in: L. C. G. PFEIFFER, Nachträge zu L. Pfeiffer *Monographia Heliceorum* [one section]. *Zeitschrift für Malakozoologie*, 6(6): 81–85 (November).  
1849z2 (December), See [1842–1852], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Turbo*).  
1849z3 (December), See [1846–1855], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Trochus*).  
1849z4 (December) {1850r, 1851f, 1852c, 1853c} [1849–1853], [Monograph on] Die Gattungen *Natica* und *Amaura*. In *Abbildungen nach der Natur mit Beschreibungen. Systematisches Conchylien-Cabinet*, 2(1): 1–66, 65[a], 66[a], 67–164, pls. A, 1–19.

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|-------|--------|-------|----------|-------|
| Pp.   | 1–18   | 19–26 |          |       |
| Pls.  | 1–6    | 7–12  | A, 13–17 | 18    |
| Date  | 1849z4 | 1850r | 1851f    | 1851f |
| Lief. | 88     | 98    | 101      | 103   |

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|-------|-------|----------------------|---------|
| Pp.   | 27–66 | 65[a], 66[a], 67–120 | 121–164 |
| Pls.  |       | 19                   |         |
| Date  | 1852c | 1852c                | 1853c   |
| Lief. | 108   | 117                  | 120     |

Collation sources: Woodward (1910: 1252); Oostingh (1925: 344); Smith & England (1937: 90); Johnson (1968: 365); Welter-Schultes (1999: 173). The latter three collations each noted that pages 65–66 were duplicated in the page numbering. Date on title page is 1852. Lief. 117 was misdated as 1851 in Welter-Schultes (1999).

1849z5, [Descriptions of some new species in]: Mollusken (Animalia Mollusca). Pp. 451–458, in: F. ROEMER, 1849, *Texas. Mit besonderer Rücksicht auf deutsche Auswanderung und die physischen Verhältnisse des Landes nach eigener Beobachtung geschildert*. Adolph Marcus, Bonn, xvi + 464 pp., 1 fold-out map [foreword dated August 1849; some land snail descriptions by L. C. G. Pfeiffer].

1850a, Diagnosen mehrerer neuer *Trochus*-Arten. *Zeitschrift für Malakozoologie*, 6(10): 146–160 (31 March); (11): 168–172 (31 March); (12): 187–192 (30 April); 7(1): 16 (30 April).

1850b, [Review of] *Die Land- und Süßwassermollusken von Java* [by Albert Mousson]. *Zeitschrift für Malakozoologie*, 7(2): 17–21 (30 April).

1850c, Bemerkung über einige Arten von *Mitra*. *Zeitschrift für Malakozoologie*, 7(2): 22–30 (30 April).

1850d, See [1844–1850], [Monograph on] *Haliotis*.  
1850e, See [1849w–1850], [Monograph on] *Fasciolaria*.  
1850f, See [1843–1850], [Monograph on] *Bulimus*.  
1850g, See [1847–1850], [Monograph on] *Lucina*.  
1850h, See [1846–1850], [Monograph on] *Cyrena*.  
\*1850, [Description of] *Helix erythrostoma*. Pp. 84–85, in: L. C. G. PFEIFFER, ed., *Beschreibungen neuer Landschnecken* [one of several sections]. *Zeitschrift für Malakozoologie*, 7(6): 81–89 (31 August).  
1850i, See [1843–1850], [Monograph on] *Arca*.  
1850j, See [1844–1850], [Monograph on] *Fusus*.  
1850k, See [1849w–1850], [Monograph on] *Fasciolaria*.  
1850-l, [Monograph on] *Galatea*. *Abbildungen und Beschreibungen*, 3(8): 123–125, pl. 1 [n. sp.: Philippi] (November 1850) [also numbered pp. 1–3].  
1850m, See [1849m–1850], [Monograph on] *Pholas*.  
1850n, [Monograph on] *Anomia*. *Abbildungen und Beschreibungen*, 3(8): 131–133, 1 pl. [misabeled as pl. 3 on pp. 132–133] [n. sp.: Philippi] (November 1850) [also numbered pp. 1–3].  
1850o, See [1844–1850], [Monograph on] *Mactra*.  
1850p, See [1842–1852], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Turbo*).  
1850q, See [1846–1855], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Trochus*).



1850r, See [1849z4–1853], [Monograph on] Die Gattungen *Natica* und *Amaura*.  
1851a, [vi] pp. Register of *Abbildungen und Beschreibungen*, Vol. 3 – January 1851 [Preface date].  
1851b, See [1849s–1851], Centuria quarta testaceorum novorum. *Zeitschrift für Malakozoologie*, 8(2): 29–32 (30 June 1851); 8(3): 39–48 (15 July 1851); 8(4): 49–64 (15 July 1851); 8(5): 65–74 (31 July 1851).  
1851c {1852a} [1851–1852], Centuria quinta testaceorum novorum. *Zeitschrift für Malakozoologie*, 8(5): 74–80 (31 July 1851); 8(6): 81–96 (31 August 1851); 8(8): 123–126 (31 December 1851); 9(2): 20–29 (25 March 1852).  
1851d {1852b} [1851–1852], [Monograph on] Die Gattung *Ampullaria*. In *Abbildungen nach der Natur mit Beschreibungen*. *Systematisches Conchylien-Cabinet*, 1(20)[(1)]: 1–74, pls. A, 1–21.

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|-------|--------|-------|-------|-------|
| Pp.   | 1–24   | 25–48 | 49–74 |       |
| Pls.  | A, 1–5 | 6–11  | 12–17 | 18–21 |
| Date  | 1851d  | 1852b | 1852b | 1852b |
| Lief. | 104    | 107   | 110   | 113   |

Collation sources: Woodward (1910: 1252); Smith & England (1937: 91); Johnson (1968: 364); Welter-Schultes (1999: 169). Date on title page is 1851.  
1851f, See [1849z4–1853], [Monograph on] Die Gattungen *Natica* und *Amaura*.  
1852a, See [1851–1852], Centuria quinta testaceorum novorum. *Zeitschrift für Malakozoologie*, 9(2): 20–29 (25 March 1852).  
1852b, See [1851–1852], [Monograph on] Die Gattung *Ampullaria*.  
1852c, See [1849z4–1853], [Monograph on] Die Gattungen *Natica* und *Amaura*.  
1852d, See [1846–1855], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Trochus*).  
1852e {1853d} [1852–1853], [Monograph of] Die Gattungen *Delphinula*, *Scissurella* und *Globulus*. In *Abbildungen nach der Natur mit Beschreibungen*. *Systematisches Conchylien-Cabinet*, 2(4): 1–57, pls. 1–8.

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|-------|--------|--------|
| Pp.   |        | 1–57   |
| Pls.  | 1–3, 5 | 4, 6–8 |
| Date  | 1852e  | 1853d  |
| Lief. | 117    | 123    |

Collation sources: Woodward (1910: 1252); Oostingh (1925: 345, but without breakdown by year); Smith & England (1937: 91); Johnson (1968: 365); Welter-Schultes (1999: 174). Date on title page is 1853.  
1852f, See [1842–1852], [Monograph on] Die Kreiselschnecken oder Trochoideen (Gattungen *Turbo*).  
1853a, *Handbuch der Conchyliologie und Malacologie*. Anton, Halle, xx + 548 pp. (pre-1 May – review in *Journal de Conchyliologie*, 4(3): 216).  
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1853d, See [1852–1853]. [Monograph of] Die Gattungen *Delphinula*, *Scissurella* und *Globulus*.  
1853e, [Monograph on] Die Gattungen *Phasianella* und *Bankivia*. *Systematisches Conchylien-Cabinet*, 2(5): 1–52, pls. 1–6.

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| Pp.   | 1–52  |
| Pls.  | 1–6   |
| Date  | 1853e |
| Lief. | 126   |

Collation sources: Woodward (1910: 1252); Smith & England (1937: 91); Johnson (1968: 365); Welter-Schultes (1999: 174). Also includes *Lacuna*.  
1853f, [Monograph on] Die Gattungen *Adeorbis*, *Skenea*, *Orbis* und *Fossarus*. *Systematisches Conchylien-Cabinet*, 2(6): 1–14, pl. 1.



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| Pp.   | 1–14  |
| Pls.  | 1     |
| Date  | 1853f |
| Lief. | 123?  |

Collation sources: Woodward (1910: 1252); Smith & England (1937: 91, only listed as "1853" with no further information); Johnson (1968: 365); Welter-Schultes (1999: 174–175). (The genus *Orbis* is a foraminiferan.)

1853g, [Monograph on] Die Gattung *Solarium*. *Systematisches Conchylien-Cabinet*, 2(7): 1–42, pls. 1–4.

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| Pp.   | 1–42  |
| Pls.  | 1–4   |
| Date  | 1853g |
| Lief. | 129?  |

Collation sources: Woodward (1910: 1252); Oostingh (1925: 345); Smith & England (1937: 91, only listed as "1853" with no further information); Johnson (1968: 365); Welter-Schultes (1999: 175).

1853h, Die Gattung *Risella*. *Systematisches Conchylien-Cabinet*, 2(8): 1–10, pl. 1.

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| Pp.   | 1–10  |
| Pls.  | 1     |
| Date  | 1853h |
| Lief. | 123?  |

Collation sources: Woodward (1910: 1252); Smith & England (1937: 91, only listed as "1853" with no further information); Johnson (1968: 365); Welter-Schultes (1999: 175). Welter-Schultes (1999: 175) noted that all texts and plates of 2(6), 2(7), and 2(8) seemed to be issued in 1853 – 2(6) and 2(8) in Lieferung 123(?) and 2(7) in Lieferung 129(?).

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|------|----------------|---------|------|
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| 2    | 11–18          | 21–40   | 1870 |
| 3    | 19–28          | 41–60   | 1872 |
| 4    | 29–34          | 61–80   | 1873 |
| 5    | 35–40          | 81–100  | 1874 |
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|       |      |      |                     |      |
|-------|------|------|---------------------|------|
| Pp.   | 1–24 |      | 23[a], 24[a], 25–30 |      |
| Pls.  | 2    | 3    |                     | 4–6  |
| Date  | 1841 | 1841 | 1843                | 1843 |
| Lief. | 25   | 30   | 41                  | 42   |

|       |        |              |       |
|-------|--------|--------------|-------|
| Pp.   | 31–46  | 47–76, V, VI |       |
| Pls.  | 1, 7–9 |              | A     |
| Date  | 1844   | 1845         | 1845? |
| Lief. | 49     | 53           | 53?   |

Collation sources: Woodward (1910: 1252); Oostingh (1925: 358); Smith & England (1937: 92); Johnson (1968: 364); Welter-Schultes (1999: 166). Date on title page is 1844. Plate A was not mentioned in Smith & England (1937), and could be issued in Lieferung 53. Plate A is quoted on page 68. Authorship erroneously given as “C. H.” Küster rather than “H. C.” Küster. Johnson (1968: 364) noted that pages 23–24 were duplicated in the page numbering. The species of *Auricula* in this work attributed by some authors to Philippi should instead be attributed to Küster, ex Philippi ms.

[KÜSTER, H. C.], 1843–1868, Mollusca Acephala. Kopflose Mollusken. *Systematisches Conchylien-Cabinet*, 7(1): 1–84, pls. 1–14, 2b–d, 6b [contains material by Philippi & Koch].

|       |           |       |       |                 |      |
|-------|-----------|-------|-------|-----------------|------|
| Pp.   |           | 1–8   | 9–24  | [Lief. Wrapper] |      |
| Pls.  | 2–4, 9–11 |       | 1, 2b | 5, 8, 12        | 13   |
| Date  | 1843      | 1843? | 1844  | 1844            | 1844 |
| Lief. | 40        | 40?   | 41    | 45              | 46   |

|       |      |            |       |      |  |
|-------|------|------------|-------|------|--|
| Pp.   |      | 25–40      | 41–84 |      |  |
| Pls.  | 7    | 2c, 2d, 14 | 6, 6b |      |  |
| Date  | 1845 | 1848       | 1858  | 1868 |  |
| Lief. | 56   | 75         | 161   | 186  |  |

Collation sources: Woodward (1910: 1253) (gave dates as “1843–”); Oostingh (1925: 358); Smith & England (1937: 97); Johnson (1968: 366); Welter-Schultes (1999: 185–186), Marshall (2002). Welter-Schultes (1999: 186) noted that pages 1–8 were not mentioned in Smith & England (1937), and contain general statements about bivalves, molluscs, and brachiopods. Küster (1843, volume 0(2)) claimed that Bogen 1–3 were already issued before Lieferung 43, so pages 1–8 (= Bogen 1) could have been issued before Lieferung 41, probably in Lieferung 40. 7(1) contains no title page with information about the publication year. No register. Contents: Brachiopoda: Lingulacea: *Lingula*; Terebratulacea: *Terebratula*, *Thecidium*, *Crania*; Conchifera: Ostracea: *Anomia*, *Aenigma*, *Placuna*, *Ostrea*. Oostingh (1925: 358) and Johnson (1968: 366) attributed the authorship of this section to H. C. Küster, with pages 61–64 and plate 7 (genus *Aenigma*) authored by “Bergrath” Koch (= F. C. L. Koch). There exists a single sheet consisting of two unpaginated pages by Koch, with a description of *Aenigma* n.g., referring to plate 7, obviously issued after October 1846 in Lieferung 56 (1845); in some



sets, these two pages are bound after page 40 of this volume. Marshall (2002), based on information on the wrapper for part 45, confirmed that part 45 was issued in 1844, not 1843, and that plate 13 was issued with part 46, not part 45.

KÜSTER, H. C. & S. CLESSIN, 1838–1876, Die Gattung *Anodonta* nebst den übrigen Najaden mit unvollkommenem Schloss. In Abbildungen nach der Natur mit Beschreibungen. Mollusca Elatobran-  
chia: Najadea, Najaden. *Systematisches Conchylien-Cabinet*, 9(1): 1–288, pls. A, 1–87, 2[a], 3[a], 4[a], 11.

|        |        |        |        |        |            |                        |  |
|--------|--------|--------|--------|--------|------------|------------------------|--|
| Pp.    | 1–16   | 17–40  |        |        | 41–64      |                        |  |
| Pls.   | A, 1–5 | 6–8    | 4[a]   | 2[a]   | 12, 25, 27 | 10, 11, 11, 14, 16, 18 |  |
| Date   | 1838   | 1839   | 1840   | 1841   | 1842       | 1853                   |  |
| Lief.  | 9      | 14     | 21     | 29     | 34         | 121                    |  |
| Author | Küster | Küster | Küster | Küster | Küster     | Küster                 |  |

|        |                   |  |         |         |         |         |         |
|--------|-------------------|--|---------|---------|---------|---------|---------|
| Pp.    | 65–88             |  | 89–112  | 113–128 | 129–144 | 145–168 | 169–176 |
| Pls.   | 17, 19, 22–24, 26 |  | 28–33   | 34–39   | 40–45   | 46–51   | 52–57   |
| Date   | 1873              |  | 1873    | 1874    | 1874    | 1874    | 1874    |
| Lief.  | 219               |  | 220     | 223     | 224     | 225     | 232     |
| Author | Clessin           |  | Clessin | Clessin | Clessin | Clessin | Clessin |

|        |         |         |         |         |         |                         |  |
|--------|---------|---------|---------|---------|---------|-------------------------|--|
| Pp.    | 177–192 | 193–216 | 217–240 | 241–264 | 265–288 |                         |  |
| Pls.   | 58–63   | 64–69   | 70–75   | 76–81   | 82–87   | 3[a], 9, 13, 15, 20, 21 |  |
| Date   | 1875    | 1875    | 1876    | 1876    | 1876    | ?                       |  |
| Lief.  | 234     | 239     | 245     | 248     | 252     | ?                       |  |
| Author | Clessin | Clessin | Clessin | Clessin | Clessin | ?                       |  |

Sources: Woodward (1910: 1253); Smith & England (1937: 93); Johnson (1968: 366); Welter-Schultes (1999: 188–189). Two title pages, one with 1838 and the other with 1876 as the date of publication. Welter-Schultes (1999: 189) noted that page 288 (errata sheet) is unpaginated. Plates 9, 13, 15, 20, and 21 were not mentioned in Smith & England (1937), different plates 2–4 were not considered. According to their similar design (“Küster ad nat. pinx.” is quoted on the pls.), plates 9, 13, and 15 should have been issued in one single Lieferung (probably around 1850–1855), plates 20 and 21 (“F. Sturm del.”) in another Lieferung. Plates 2–4 are not preserved in Göttingen, they were “replaced” by other plates 2[a]–4[a] a few years later. Plate 4[a] was issued in Lieferung 21, plate 2[a] in Lieferung 29, both dates according to notes on the wrappers, plate 3[a] must have been issued in one of the following Lieferungen. Lieferung “222” in Smith & England (1937) obviously a printing error, correct is 223 according to the wrapper.

KÜSTER H. C. & S. CLESSIN, 1840–1890, Die Familie Mytilidae. In Abbildungen nach der Natur mit Beschreibungen. Mollusca Elatobran-  
chia: Mytiloidea; Miesmuscheln. *Systematisches Conchylien-Cabinet*, 8(3): 1–170, pls. 1–36.

|        |        |        |         |         |         |           |
|--------|--------|--------|---------|---------|---------|-----------|
| Pp.    | 1–8    | 9–12   | 13–28   | 29–60   | 61–76   | 77–92     |
| Pls.   | 1, 3–5 | 2, 6   | 7–12    | 13–18   | 19–21   | 22–24, 26 |
| Date   | 1840   | 1841   | 1886    | 1887    | 1887    | 1887      |
| Lief.  | 21     | 29     | 344     | 345     | 347     | 351       |
| Author | Küster | Küster | Clessin | Clessin | Clessin | Clessin   |

|        |         |         |         |         |         |
|--------|---------|---------|---------|---------|---------|
| Pp.    | 93–116  | 117–124 | 125–132 | 133–156 | 157–170 |
| Pls.   | 27–32   | 25      | 33, 34  | 35, 36  |         |
| Date   | 1887    | 1887    | 1888    | 1889    | 1890    |
| Lief.  | 352     | 353     | 361     | 372     | 376     |
| Author | Clessin | Clessin | Clessin | Clessin | Clessin |



Collation sources: Woodward (1910: 1253); Oostingh (1925: 359); Prashad (1932: 4); Smith & England (1937: 95); Johnson (1968: 366); Welter-Schultes (1999: 187–188). Date on title page is 1889.

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|        |        |        |           |           |           |
|--------|--------|--------|-----------|-----------|-----------|
| Pp.    |        | 1–24   | 25–40     | 41–72     | 73–114    |
| Pls.   | 1–2    | 3–5    |           | 6–11      | 12–14     |
| Date   | 1853   | 1856   | 1878      | 1882      | 1882      |
| Lief.  | 129    | 149    | 269       | 315       | 318       |
| Author | Küster | Küster | Weinkauff | Weinkauff | Weinkauff |

Collation sources: Woodward (1910: 1252); Smith & England (1937: 94); Johnson (1968: 365); Welter-Schultes (1999: 175). Two title pages, one with “1856,” and the other with “1882” as the publication date.

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| Volume | Heft | Pages                    | Plates | Date             |
|--------|------|--------------------------|--------|------------------|
| 1      | 1    | vi + 1–132               | 1–5    | ≥ April 1835     |
|        | 2    | [6] + 1–26               | 6–10   | ≥ August 1835    |
|        | 3    | [4] + 1–33               | 11–15  | ≥ March 1836     |
|        | 4    | [4] + 1–27               | 16–20  | ≥ September 1836 |
|        | 5–6  | [4] + 1–70 + title page  | 21–30  | ≥ July 1837      |
| 2      | 7–8  | [4] + 1–44               | 31–40  | ≥ Jun. 1838      |
|        | 9–10 | iv + 1–46                | 41–50  | ≥ September 1839 |
|        | 11   | iv + 1–15                | 51–55  | ≥ Jun. 1842      |
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## LETTER FROM THE EDITOR







## LETTER FROM THE EDITOR

After 42 extraordinary years of distinguished service, Dr. George Davis has decided to retire as Editor-in-Chief of *Malacologia*. After some discussion with the Board of Directors of the Institute of Malacology and a consultative visit to Cape Cod, Massachusetts, with George to learn the tricks of the trade, I have agreed to become the next Editor-in-Chief. I have been studying freshwater molluscan (cerithioidean gastropods/unionid bivalve) systematics and dabbling in terrestrial gastropod faunal surveys for the past 24+ years. Fortunately, the Copy Editor (Eugene V. Coan), Composition Editor (Claudia Wilke), Associate Editor (John B. Burch) and Associate Editor (Thomas Wilke) have all agreed to continue in their valued role for the Institute of Malacology. One additional change, however, that will take place is we will be transitioning from Caryl Hesterman as Managing Editor to David C. Campbell. David is an accomplished malacologist and collaborator of mine, who has the attention to detail that is required for the job. We all extend a hearty thanks to Caryl for her 30 years of exemplary service to *Malacologia*.

As Editor-in-Chief, I am implementing, effective immediately, some modest procedural changes in *Malacologia* to give a greater role to the associate editors, as is the case with most scientific journals. Typically, a manuscript is submitted to the editor, who then sends the manuscript to an associate editor with expertise in a salient topic area. That associate editor chooses external reviewers, receives those reviews and makes a recommendation for publication, or otherwise, to the editor. I feel

this new, decentralized approach will result in greater exposure of the journal to future prospective authors and will act to strengthen the journal. It will also provide the associate editors with a stronger sense of oversight for the articles being published. This volume lists the names of the current individuals who have agreed to continue to serve on the Board of Associate Editors as associate editors in manner I have described. I very much appreciate their willingness to continue to serve and welcome new members Drs. Shawn McLaughlin, Wallace Meyer and Rebecca J. Rundell. Special thanks are in order to retiring Editorial Board members Drs. John Allen, Thierry Backeljau, Philippe Bouchet, Joseph Carter, Elaine Hoagland, Cristián Ituarte, Michael Johnson, Gennady Kamenev, Yuri Kantor, Takaki Kondo, Takashi Okutani, Richard Pipe, Winston Ponder, Takenori Sasaki, Peter Tattersfield, Anders Warén and Shi-Kuei Wu for their many years of service on the Board.

I am following an August lineage of General Editors/Editors-in-Chief with Anne Gismann serving from 1962 to 1968, Anne Gismann and John B. Burch serving 1969, John B. Burch serving from 1970 to 1974, George Davis and Robert Robertson serving from 1975 to 1988, and finally George Davis acting alone as Editor-in-Chief from 1988 to 2016. I come nowhere close to having accomplished what they have done over the years as malacologists, but believe with the help of my extraordinary team we will continue to produce a premier international journal that contributors and readers alike will take pride in.

Sincerely,

Charles “Chuck” Lydeard  
Editor-in-Chief







|                  |              |
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| Vol. 50, No. 1–2 | 9 June 2008  |
| Vol. 51, No. 1   | 19 Mar. 2009 |
| Vol. 51, No. 2   | 26 Aug. 2009 |
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| Vol. 55, No. 1   | 17 Sep. 2012 |
| Vol. 55, No. 2   | 28 Dec. 2012 |
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For a full list of the publication dates of *Malacologia* up to 2008, see:

Coan, E. V., 2008, Publication dates of *Malacologia* volumes and issues. *Malacologia*, 50(1–2): 361.

Also see:

[http://www.malacological.org/downloads/epubs/2400-years/2400collations\(journals\).pdf](http://www.malacological.org/downloads/epubs/2400-years/2400collations(journals).pdf)



## INSTRUCTIONS FOR AUTHORS

1. MALACOLOGIA publishes original research on the Mollusca that is of high quality and of broad international interest. Papers combining synthesis with innovation are particularly desired. While publishing symposia from time to time, MALACOLOGIA encourages submission of single manuscripts on diverse topics. Smaller papers of local geographical or systematic content, and of high quality and interest, may be accepted as 'Research Notes'. Nearly all branches of malacology are represented in the pages of MALACOLOGIA.
2. Manuscripts submitted for publication are received with the tacit understanding that they have not been submitted or published elsewhere in whole or in part.
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4. Unless indicated otherwise below, contributors should follow the recommendations in the Council of Science Editors (CSE) Scientific Style and Format manual, 8<sup>th</sup> ed., 2014 (ISBN 9780226116495).
5. Be brief.
6. Manuscripts must be prepared using Microsoft Word® (Windows-version), Arial, 12 point font size, lines at 1.5 spaces throughout (including references, tables and figure captions), no added spaces before or after paragraphs, text aligned left. Tables, figure captions and figures are to be placed on separate pages at the end of the file. Make the hierarchy of headings within the text simple and consistent. Avoid internal page references.
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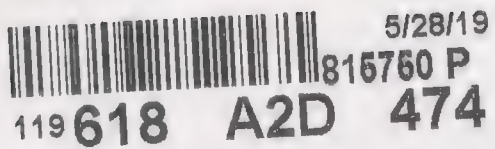
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